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1 **Relative importance of environmental factors and farming**
2 **practices in shaping weed communities structure and composition**
3 **in French vineyards**

4

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22

23 **Abstract**

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

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

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

52

53 **1. Introduction**

54 Promoting biodiversity in agrosystems, combined with a reduced dependence on pesticides has
55 become a key issue in agriculture over recent years (Altieri, 1999; Feledyn-Szewczyk *et al.*, 2016).
56 Among taxa associated with cultivated land, weed species may play an important role in maintaining
57 biodiversity, as long as their adverse effects on crop production are limited (Marshall *et al.*, 2003;
58 Storkey, 2006). In order to achieve this goal, a thorough understanding of the relative importance of
59 biotic, abiotic and anthropogenic factors, acting as filters for species assemblages in weed
60 communities is needed (Belyea and Lancaster, 1999). Specifically, improving the knowledge about
61 how environmental factors and management practices influence the variations of weed community
62 composition and structure is an essential first stage in developing alternative weed control
63 management practices at both the field and the landscape scales (Michez and Guillermin, 1984).
64 Vineyards are an ideal study model as flora management practices have become more diversified in
65 recent years (Gago *et al.*, 2007). Before the 1970s, vegetation in- and between vine rows was
66 traditionally managed by soil tillage (Barralis *et al.*, 1983; Maillet, 1992). The generalized use of
67 chemical weed control then induced important changes in composition and richness of weed
68 communities between the 1970s and the 1990s (Barralis *et al.*, 1983; Maillet, 1992; Monteiro *et al.*,
69 2008). Herbicide application has caused shifts in weed flora composition due to the progressive
70 removal of herbicide sensitive species that has led to an overall reduced species richness and to the
71 progressive increase of some tolerant species (physiologically) or species able to escape (temporally)
72 the treatments (Dastgheib and Frampton, 2000; Baumgartner *et al.*, 2007; Gago *et al.*, 2007;
73 Sanguankeo *et al.*, 2009). Besides the effect of herbicides per se, the timing of their application can
74 also shift the weed community, especially if applied when weeds are less susceptible to chemical
75 control (Baumgartner *et al.*, 2007). Nowadays, herbicide treatments in vineyards are usually restricted

76 to the vine rows (which represents from 10 to 15% of the total vineyard surface area), and can involve
77 pre-emergence and/or post-emergence herbicides (Dastgheib and Frampton, 2000). Frequently tilled
78 rows and inter-rows represent highly disturbed habitats which often harbour communities with a small
79 number of species but with a large variability in species abundance (Wilmanns, 1989, 1993; Kazakou
80 *et al.*, 2016). More recently, weed control in vineyards is being provided by establishing a cover crop
81 (Baumgartner *et al.*, 2008). Besides their effect on weeds, cover-crops in vineyards are primarily used
82 as leverage to confront various agronomic issues such as poor soil organic carbon levels, erosion and
83 fertility losses (Salome *et al.*, 2016, Garcia *et al.*, 2018). Sometimes, spontaneous vegetation can be
84 preferred as it provides a low cost intercropping option and may offer interesting trade-offs between
85 ecosystem services (Kazakou *et al.*, 2016). Whatever the case (spontaneous vegetation or cover crop),
86 the vegetation is then mown. In conclusion, three main weed management methods co-exist in
87 vineyards: soil tillage, herbicide applications and mowing. In addition to farming practices, the weed
88 composition of vineyards can be affected by environmental factors such as soil or climate, related to
89 species ecological preferences. Weed flora is also characterized by a seasonal dynamic, related to the
90 differences in species requirements for temperature and precipitation to germinate and complete their
91 life cycle.

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

103 soil tillage practices.

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

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

117 **2. Material and methods**

118 **2.1. Study regions**

119 As part of the Biovigilance Flore national arable weed survey conducted in France, mainly on annual
120 crops (see Fried *et al.* (2008)), specific surveys were also performed in vineyards between 2006 and
121 2012. The vineyard vegetation surveys covered three main wine production regions: i) Languedoc, ii)
122 Beaujolais and northern Rhône valley and iii) Champagne, covering a diversity of pedo-climatic
123 conditions and management practices from the south to the north of France (Figure 1). Languedoc has
124 a Mediterranean climate with a mean annual temperature of 14.1°C, and 686 mm annual rainfall in the
125 surveyed plots, based on WorldClim database (Hijmans *et al.*, 2005). The Treatment Frequency Index
126 (TFI) for herbicides, i.e. the cumulative ratio of the dose applied to the recommended dose, for all
127 treatments applied during the growing season (Halberg, 1999), ranged between 0.4 in 2006 to 0.5 in
128 2013 (Pujol, 2017) with a mean of 0.48 in our surveyed plots. Permanent or temporary sown or

129 spontaneous cover crops in the inter-rows are only observed in 29% of the Languedoc vineyards
130 (Agreste, 2009) but in only 10.2% of our surveyed plots in this region. Beaujolais and northern Rhone
131 valley have a semi-continental climate with temperate influences, with a mean annual temperature of
132 11.4°C and 776 mm annual rainfall in the surveyed plots. The TFI for herbicides ranged between 1.1
133 in 2006 to 1.2 in 2010 (Pujol, 2017), with a mean of 1.38 in our surveyed plots. In this region, 42% of
134 the vineyards display a cover crop in the inter-rows (Agreste, 2009) with 40.6% of the surveyed plots
135 with cover crops. Finally Champagne has a continental climate with oceanic influences, with a mean
136 annual temperature of 10.1°C and 657 mm annual rainfall. The TFI for herbicides ranged between 1.2
137 in 2010 to 1.4 in 2013 (Pujol, 2017) with 1.24 on the rows of our surveyed plots. Only 26% of the
138 vineyards have cover crops in this region (Agreste, 2009) but 62.5% in our surveyed plots. The
139 Biovigilance sampling represented the mean level of herbicide treatments well in each region,
140 however in terms of cover crops, Biovigilance was only representative in Beaujolais and the northern
141 Rhone valley while cover crops were under-represented in Languedoc (10.2% against 29%) and over-
142 represented in Champagne (62.5% against 26%).

143 **2.2. Vegetation surveys**

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

156 The abundance of each species was estimated using five abundance classes as developed in
157 (Barralis, 1976). This method takes into account the number of individuals per m^2 , using the following
158 scale intervals: '1' less than 1 individual/ m^2 ; '2' 1–2 individuals/ m^2 ; '3' 3–20 individuals/ m^2 ; '4'
159 21–50 individuals/ m^2 ; '5' more than 50 individuals/ m^2 . At the community-level, we calculated
160 species richness (S), the number of species in a sampling unit, and total abundance that we defined as
161 the sum of the abundance of each species present in a sampling unit. For this purpose, we transformed
162 the abundance class into a quantitative scale using the median of the range of density associated with
163 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
164 ind/ m^2).

165 **2.3. Explanatory variables**

166 Explanatory variables can be grouped into four types: i) spatial variables, ii) environmental conditions,
167 iii) management practices and iv) temporal variables. To account for the spatial component of
168 variability (see Borcard *et al.* (1992)), spatial variables were constructed by using longitudinal x and
169 latitudinal y coordinates of the studied vineyards. First (x, y), second (x^2, y^2) and third (x^3, y^3) order
170 terms of the spatial coordinates were created for the analyses, along with interaction terms (xy^2, x^2y).
171 Second and third order terms were included in order to account for more complex, patchy spatial
172 patterns in community composition or diversity to be detected (Legendre and Legendre, 1998).
173 Detailed soil analyses were only available for 14 plots (30% of the plots). Therefore, we retrieved 8
174 factors from the Soilgrids dataset at 250m resolution (Hengl *et al.*, 2017) based on the coordinates of
175 the vineyard plots. There was a high correlation between available soil parameters and those estimated
176 from the Soilgrids dataset (e.g. pH, $r=0.86$). We performed a principal component analysis (PCA) on
177 the 7 soil variables (which included : soil organic carbon content, pH index measured in water
178 solution, bulk density (fine earth) in kg per cubic meter, CEC (Cation Exchange Capacity of soil),
179 weight percentage of the sand particles (0.05–2 mm), weight percentage of the silt particles (0.0002–
180 0.05 mm), weight percentage of the clay particles (<0.0002 mm), volumetric percentage of coarse
181 fragments (>2 mm)) and extracted the three first axes, which represented 82% of total inertia and were
182 associated to a gradient of soil pH on axis 1 and to soil texture gradient on axis 2 and 3, opposing

183 sandy soils to silty soils on axis 2 and clay soils to sandy soils on axis 3, respectively (see Appendix
184 S1 for the detail outputs of the PCA). Winegrowers were asked about vegetation management along
185 the rows (R) and the inter-rows (IR) for the years covered by the survey. Three main types of
186 management practices can be distinguished: mowing (including crushing), soil tillage and chemical
187 treatments with herbicides. The main types of soil tillage implemented in our survey included “rasette”
188 (25%), rotary inter-vine hoes (15%) and mouldboard plough (8%), with a typical working depth
189 between 5-15 cm. Glyphosate represented the main herbicide used (61.2%) followed by aminotriazole
190 (13.3%) and glufosinate (8.5%). Table 2 summarizes the main trend in the management practices in
191 each region. Different management practices or combinations are employed on the R and the IR and
192 management practices differ also on the same vineyard plot over the years. Thus, to summarize
193 management practices of each year in each vineyard, we used the number of mowings, of soil tillings
194 and of herbicide treatments per year. We also distinguished management practice types and the
195 different combinations of management practices applied to the rows and to the inter-rows: 1-
196 herbicides only (H), 2- soil tillage only (T), 3-mix of herbicides and soil tillage (HT), 4- mix of soil
197 tillage and mowing (TM). Temporal variations in vineyard flora were assessed with two variables: the
198 date of the vegetation sampling (Julian Day) that account for seasonal variation in weed flora
199 (hereafter called ‘Season’) and the year which could account for particular weather conditions. Table 3
200 gives the units and ranges of the raw variables used in the study.

201 **2.4. Data analysis**

202 Frequency of occurrence of species was compared between the rows and the inter-rows using a fidelity
203 measurement, which reflects the concentration of species occurrence in different habitats (Chytrý *et*

204 *al.*, 2002). We used the phi coefficient of association $\Phi = \frac{N.n_p - n.N_p}{\sqrt{n.N_p.(N-n).(N-N_p)}}$

205 with N the total number of samples used (883), N_p , the number of samples in the rows (449), n, the
206 number of occurrences of the species in the whole dataset and n_p the number of occurrences of the
207 species in the rows. This index ranged from -1 (species associated to inter-rows) to +1 (species
208 associated to rows). For the three different regions, we also computed species ranking based on their

209 frequency of occurrence in the vineyard plots. In this latter case, for the sake of simplicity we did not
210 distinguish between rows and inter-rows (i.e., a species is considered to occur in a vineyard plot as
211 long as it is present in either the row or the inter-row).

212 To analyze the relationship between explanatory variables and vegetation composition, we
213 used a constrained ordination method that was applied separately on the two areas (rows and inter-
214 rows). Before analysis, species abundance data were square-rooted. An indirect model (Detrended
215 Correspondence Analysis, DCA) was first used to decide whether to use a linear or a unimodal
216 approximation (Ter Braak and Šmilauer, 2002; Lepš and Šmilauer, 2003). These DCA revealed that
217 the rate of turnover of plant taxa across the sites on the first axis of variation was such that a unimodal
218 model assumption would be more appropriate than a linear model assumption (DCA axis 1 length =
219 4.43 in the inter-rows, DCA axis 1 length = 4.43 in the rows). Therefore, Canonical Correspondence
220 Analysis (CCA) was undertaken between the vegetation assemblage data and the 16 explanatory
221 variables. Collinearity issues were checked with a variation inflation factor (VIF) with an initial CCA
222 including all 16 explanatory variables. VIF values of 10 or higher are usually interpreted as revealing
223 severe multicollinearity issues (Hair *et al.*, 2006). At this step, three variables with $VIF > 10$ were
224 removed (x^3 , y^2 , y^3) for both row and inter-row datasets. Correlation among the 13 remaining variables
225 can be visualized in Appendix S2. We further reduced the number of explanatory variables by
226 performing a backward and a forward selection of explanatory variables based on *P*-value using
227 function `ordistep` of package `vegan` (Oksanen *et al.*, 2017).

228 We then compared the gross and net effects of each explanatory variable, following the
229 methodology described in Lososová *et al.* (2004). The gross effects represented the variation
230 explained by a 'univariate' CCA containing the predictor of interest as the only explanatory variable.
231 The net effect of each particular variable after partitioning out the effect shared with the other
232 explanatory variables (also called conditionals) was tested with a partial CCA (pCCA). We extracted
233 the explained variance and the adjusted R-squared for models of both gross and net effects of each
234 variable retained in the reduced models. In models of net effects, model fit was also assessed by the F-
235 value for which a type I error rate was estimated using 999 permutation tests of the constrained axis.
236 The importance of each explanatory variable was ranked using the values of the pCCA (i.e. net effect)

237 models. Subsequently, we identified the 10 species with the highest fit for the best explanatory
238 variable of each group of variables (i.e., spatial, temporal, soil and management). Species fit on the
239 constrained ordination axes was calculated using the ‘goodness’ function of the vegan package.

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

256

257 **3. Results**

258 Across the 883 surveys from 46 vineyard plots (in both rows and inter-rows), a total of 234 species
259 were recorded of which 56 were found in the three winegrowing regions. The ten most frequent
260 species (based on the 883 samples) included: *Convolvulus arvensis* (45.3%), *Cirsium arvense* (38.5%),
261 *Senecio vulgaris* (37.0%), *Diplotaxis eruroides* (30.4%), *Geranium rotundifolium* (27.7%), *Erigeron*
262 *canadensis* (25.4%), *Taraxacum officinale* (24.5%), *Crepis sancta* (24.5%), *Lactuca serriola* (21.3%)
263 and *Sonchus oleraceus* (20.8%). Appendix S3 gives the 30 most frequent species with their detailed

264 frequency in the rows and the inter-rows, as well as their frequency and rank in the three regions and
265 their status (native/alien). Some species such as *Convolvulus arvensis*, *Senecio vulgaris*, *Cirsium*
266 *arvense* and *Geranium rotundifolium* were widespread in all three regions while the top ranked species
267 (based on frequency) in each regions differed sometimes markedly with *Diploaxis erucoides* and
268 *Sonchus oleraceus* in Languedoc, *Erigeron canadensis* and *Veronica persica* in the Rhone valley and
269 *Taraxacum officinale* and *Poa annua* in Champagne (Appendix S3). The vineyard flora was composed
270 of 85% native species, 6% archaeophytes (*i.e.* alien species introduced before 1500) and 8% neophytes
271 (*i.e.* alien species introduced after 1500). The most frequent neophytes included *Erigeron canadensis*,
272 *Crepis sancta* and *Veronica persica* while *Papaver rhoeas* was the most frequent archaeophyte. The
273 mean relative abundance of alien species (archaeophytes + neophytes) at the 2000m² quadrat scale
274 varied from 8% in Champagne to 24% in Rhone valley and 14% in Languedoc.

275 Most species (79%) are found in both rows and inter-rows with only 20 (9%) and 29 (12%)
276 species only present in the rows or in the inter-rows, respectively. The fidelity index to the rows
277 ranged between 0.197 for *Rubia peregrina* (the species most associated to the rows) and -0.160 for
278 *Trifolium repens* (the species most associated to the inter-rows). Among common species, *Diploaxis*
279 *erucoides* (-0.129), *Poa annua* (-0.101), *Plantago lanceolata* (-0.076) and *Taraxacum officinale* (-
280 0.073) were more frequent in the inter-rows while *Convolvulus arvensis* was more frequent in the
281 rows (0.080). Globally the range of values of fidelity to the rows (-0.160, 0.197) compared to maximal
282 potential values (-1, 1) showed that species are mostly present in both areas.

283 **3.1. Factors affecting weed community composition**

284 For the grapevine inter-rows, the selection procedure removed two variables: number of mowings and
285 x^2y . The reduced model with 11 variables explained 16.69% of total inertia against 17.32% for the full
286 model. The amount of variation in species composition explained by the net effects of particular
287 variables, as detected by partial CCAs (Table 4), was highest for season and decreased first through
288 latitudinal (y) and longitudinal (x^2) spatial variables, second through soil pH and year, and was lowest
289 for management variables, with the number of soil tillings explaining the highest variations among
290 management practices. The first two CCA axes explained 6.04% and 2.97% respectively. On CCA

291 axis 1, weed species composition was mainly discriminated according to latitude (-0.977) and soil pH
292 (0.728) and secondly according to longitude (-0.639), interaction between longitude and latitude (xy^2 , -
293 0.480), and the proportion of silt (-0.608, Figure 2a). Species negatively associated with axis 1 (*Malva*
294 *sylvestris*, *Calendula arvensis* or *Diploaxis eruroides*) were associated to the plots located in southern
295 France in the Languedoc vineyard, on basic clay soils while species characteristics of Champagne, on
296 more silty and neutral soils were positively associated to CCA axis 1, e.g. *Poa annua*, *Taraxacum*
297 *officinale*, or *Mercurialis annua* (Figure 2a). The second axis was to a very large degree dependent on
298 sampling date (-0.813, with early samplings on the positive loadings) and to a lesser extent to
299 longitude (0.316), soil pH (-0.297), percent of silt (-0.293) and the number of soil tillings (-0.249).
300 Species with early life cycles, typical to early spring are on positive loadings (*Crepis sancta*,
301 *Cardamine hirsuta*, *Capsella bursa pastoris*) while summer therophytes are on positive loadings
302 (*Digitaria sanguinalis*, *Heliotropium europaeum*, *Portulaca olearacea*, Figure 2a).

303 For the grapevine rows, the selection procedure kept all 12 initial variables and 16.07% of the
304 total inertia was explained. As for the inter-rows, the amount of variation in species composition in
305 grapevine row vegetation which was explained by the net effects of particular variables is highest for
306 season and decreased first through latitude, second through longitude and soil texture (sand versus
307 clay) and management variables, and is lowest for year (Table 4). The first two CCA axes showed
308 5.06% and 2.91% respectively. Similarly to the CCA analysis for inter-row vegetation, the row
309 vegetation was discriminated on CCA axis 1 according to the spatial variables (latitude (-0.934),
310 longitude (-0.794) and their interactions) as well as soil pH (0.817, Figure 3b). This first axis was also
311 constrained by the number of herbicide treatments (-0.531). *Diploaxis eruroides*, *Avena sterilis* and
312 *Sonchus oleraceus* were associated to Languedoc region on basic clay soils with no or few herbicide
313 treatments on the rows, while *Poa annua*, *Lamium purpureum* and *Anisantha sterilis* were associated
314 to more acidic, silt loam or sandy loam soils with a higher number of chemical treatments on the rows.
315 The second CCA axis opposed vineyard rows according to sampling date (-0.876) and number of soil
316 tillings (-0.409). *Arenaria serpyllifolia*, *Crepis sancta*, *Fumaria officinalis* were associated to early
317 sampled rows with little soil tillage while *Convolvulus arvensis*, *Amaranthus retroflexus* or *Equisetum*

318 *ramosissimum* where associated with late sampled rows with several soil tillings (Figure 3a). Species
319 ranks along the main gradients identified by partial CCA on the rows and the inter-rows are
320 summarized in Table 5a and 5b.

321 **3.2. Factors affecting weed communities structure (richness and abundance)**

322 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
323 inter-row (min=1, max=28). Species richness differed according to management practices in the inter-
324 rows (Kruskal-Wallis test, $P < 0.001$): there were no significant differences of species richness between
325 inter-rows where herbicides were applied (7.55 ± 4.73), inter-rows that were tilled (9.00 ± 5.84) or inter-
326 rows that were both treated with herbicides and tilled (8.80 ± 6.28), while inter-rows that were mown
327 and tilled showed the highest level of richness (12.45 ± 5.66 , Figure 4a). Total abundance showed
328 similar variations between the management practices (Kruskal-Wallis test, $P < 0.001$) with highest
329 species density for mown/tilled inter-rows and lowest for chemical and/or mechanical control methods
330 (Figure 4b).

331 The model selection procedure kept 5 variables to explain the species richness in inter-rows
332 (see Appendix S4 for detailed output of the model). The marginal R^2 of the final model (for fixed
333 factors) was 0.248 and the conditional R^2 (including the fixed factors and the random effect of plot
334 identity) was 0.369 (against 0.264 and 0.378 for the full model). The standardized effect size was
335 highest for soil pH, followed by percentage of silt, year, number of herbicide treatments and number
336 of soil tillings (Figure 5a). These two management variables were only slightly negatively correlated (-
337 0.3) for the inter-rows, showing a tendency to use one or the other practice, even if winegrowers could
338 implement both practices in the same field the same year.

339 To explain species abundance in inter-rows, the model selection procedure kept 5 variables
340 (see Appendix S5 for detailed output of the model). The marginal R^2 of the final model (for fixed
341 factors) was 0.194 and the conditional R^2 (including the fixed factors and the random effect of plot
342 identity) was 0.377 (against 0.210 and 0.382 for the full model). The standardized effect size was
343 highest for percentage of silt and year, followed by the number of herbicide treatments, season and the

344 number of soil tillage (Figure 5b). In summary, species richness and abundance in the inter-rows
345 increased with the percentage of silt and decreased with year and the number of herbicide treatments
346 applied per year and to a lesser degree with the number of soil tillings implemented each year. Species
347 richness also increased with decreasing pH and abundance decreased with growing season (higher in
348 spring, lower in autumn).

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

354 On the grapevine rows, the model selection procedure for explaining species richness kept six
355 variables (see Appendix S6 for detailed output of the model). The marginal R^2 (for fixed factors) was
356 0.215 and the conditional R^2 (including the fixed factors and the random effect of plot identity) was
357 0.372 (against 0.247 and 0.380 for the full model). The standardized effect size was highest for
358 latitude, followed by longitude square rooted terms, number of herbicide treatments, year, season and
359 number of soil tillings (Figure 6a). To explain species abundance in rows, the model selection
360 procedure kept 5 variables (see Appendix S7 for detailed output of the model). The marginal R^2 of the
361 final model (for fixed factors) was 0.210 and the conditional R^2 (including the fixed factors and the
362 random effect of plot identity) was 0.298 (against 0.219 and 0.308 for the full model). The
363 standardized effect size was highest for year, followed by x^2 , and then by the season, percentage of silt
364 and the number of herbicide treatments (Figure 6b).

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

370

371 **4. Discussion**

372 With a total of 234 species recorded in our study, we covered about 25% of the plant species diversity
373 found in French vineyards which is estimated at 900 species (Maillet, 2006). Such coverage was
374 expected due to the extent of the survey limited to three regions and above all to the classical log-
375 normal distribution of plant species with a few common species and a lot of rare species with a narrow
376 distribution. However, our survey was representative of the distribution and the responses of the main
377 weed species of the French vineyard including the 44 species considered as potentially noxious
378 (Maillet *et al.*, 2001). The total explained variation in plant composition is about 16-17%. This
379 percentage of explained variance is consistent with previous studies on plant community in arable
380 fields (Fried *et al.*, 2008) or field margins (Cordeau *et al.*, 2010). The proportion of explained
381 variation is a consequence of the large data set (883 samples x 234 species), resulting in a high amount
382 of noise (Lososová *et al.*, 2004). Although this represents a relatively low amount of explanation, it
383 allowed us to measure the relative contribution of individual variables that helped shaping the plant
384 community and to assess the relative effect of management and environmental factors (Nagy *et al.*,
385 2018).

386 **4.1 Contribution to plant assemblages of temporal and spatial characteristics of the plots**

387 Season was the strongest driver of the plant assemblages in French vineyards. The succession of
388 different species assemblages during the growing season, with the succession of spring communities
389 (*Cardamine hirsuta*, *Crepis sancta*, *Veronica* spp.) followed by summer communities (*Amaranthus*
390 spp., *Chenopodium album*, *Setaria* spp.) is well known in cultivated fields (Kropáč *et al.*, 1971;
391 Lososová *et al.*, 2006; Šilc and Čarni, 2007). This is mainly a consequence of variation in species time
392 of emergence (Roberts and Feast, 1970) related to different physiological requirements of temperature
393 and humidity for seed germination (Jauzein, 1986). In vineyards, which are characterized by large
394 spaces between rows and most generally with no cover crops in the inter-rows, such seasonal
395 dynamics was expected to be higher compared to annual crops where the shade of crop canopy
396 prevents new germinations in the course of the growing season (Andrade *et al.*, 2017). In addition, in
397 our analysis the season not only covers the variation of weather over the year but probably also

398 includes the differences of vegetation before and after management (mowing, herbicides, tillage), as
399 soil management practices are usually applied between the first census in spring and the following
400 censuses in summer/autumn. This could be important, all the more that certain practices such as tillage
401 are known to stimulate new germination (Cordeau *et al.*, 2017a) and because tillage operations are
402 more spread over the season in vineyards than in annual crops (concentrated in fallow period).

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

417 **4.2 Contribution of management practices of the plots to plant assemblages**

418 In our study, farming practices explained a low variation of plant composition. This is not in
419 accordance with previous studies in vineyards where, species composition varied more by
420 management (i.e. 49.5%) than by seasonal changes (i.e. 22.6%) (Lososová *et al.*, 2003). However, it is
421 important to mention that in the study of Lososová *et al.* (2003), the observed plant composition shifts
422 were associated with the transition from intensive agricultural management with frequent tilling and
423 herbicide use, to a more environment- friendly management by mulching. This was not the case in our

424 study, where farming practices were more homogeneous (herbicides were largely used, see Table 2)
425 and considered to be consistent over the 7 years in the surveyed plot.

426 Despite a low explanatory power, our results concerning the number of herbicide treatments or
427 the number of soil tillings are consistent with the knowledge of species biology and behaviour.
428 *Sorghum halepense* and *Malva sylvestris* seems to be associated with fields where rows received high
429 amounts of herbicide. This is in accordance with the fact that glyphosate (the most frequently used
430 herbicide in the survey) was reported to show reduced efficacy against these species, e.g. in Greece
431 (Travlos *et al.*, 2014). *Malva* spp. are considered to be naturally tolerant to glyphosate (Michael *et al.*,
432 2009), while the extensive underground rhizome of *Sorghum halepense* make it difficult to control
433 even with such systemic herbicides. At the opposite side of the herbicide intensity gradient, rows that
434 received no or very few herbicide treatments harbour species such as *Calendula arvensis* or *Muscari*
435 *comosum* that were typically considered as decreasing since the large adoption of systemic herbicides
436 in vineyards (Barralis *et al.*, 1983). Inter-rows that are poorly or not tilled are associated with higher
437 abundance of perennial species such as *Trifolium repens*, *Lepidium draba* or *Rumex pulcher*, while
438 regular soil tillage typically favours annual species such as *Cerastium glomeratum* or *Galium aparine*
439 subsp. *aparine*. Globally our results are consistent with the idea that herbicide and tillage are strong
440 filters of plant communities favouring mostly therophytes, or some perennials with high vegetative
441 reproduction capacity through cuttings (tillage, e.g. *Convolvulus arvensis*) or deep and extensive root
442 systems (herbicide e.g. *Sorghum halepense*). Whereas mowing appears to be a weaker management
443 filter that allows the presence of a greater diversity of species (Kazakou *et al.*, 2016).

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

450 **4.3. Importance of environmental and management practice filters**

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

468 **4.4. Management implications**

469 Species richness has been recently proposed as a good indicator of diversified and sustainable
470 cropping systems less prone to dominance by highly adapted resistant weed species (Storkey and
471 Neve, 2018). In this regard, our study showed that herbicides were the less sustainable management
472 practices with lower species richness and a strong decrease with increasing number of treatments.
473 Whereas mechanical control (in rows) and combination of mowing and soil tillage (in the inter-rows,
474 i.e. usually this corresponds to a temporary spontaneous cover) showed the highest species richness.
475 As already reported by Storkey and Neve (2018), the plots with the higher number of herbicide
476 treatments are also those with the most troublesome weeds such as *Sorghum halepense* or *Malva*

477 *sylvestris*. Finally, managing rows and inter-rows with different tactics may create different habitats at
478 the field level and select species with different response traits, enhancing the overall weed species
479 richness at the vineyard plot scale.

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

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

504 **4.5. Conclusions**

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

515

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522

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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 containing 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 containing 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

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.

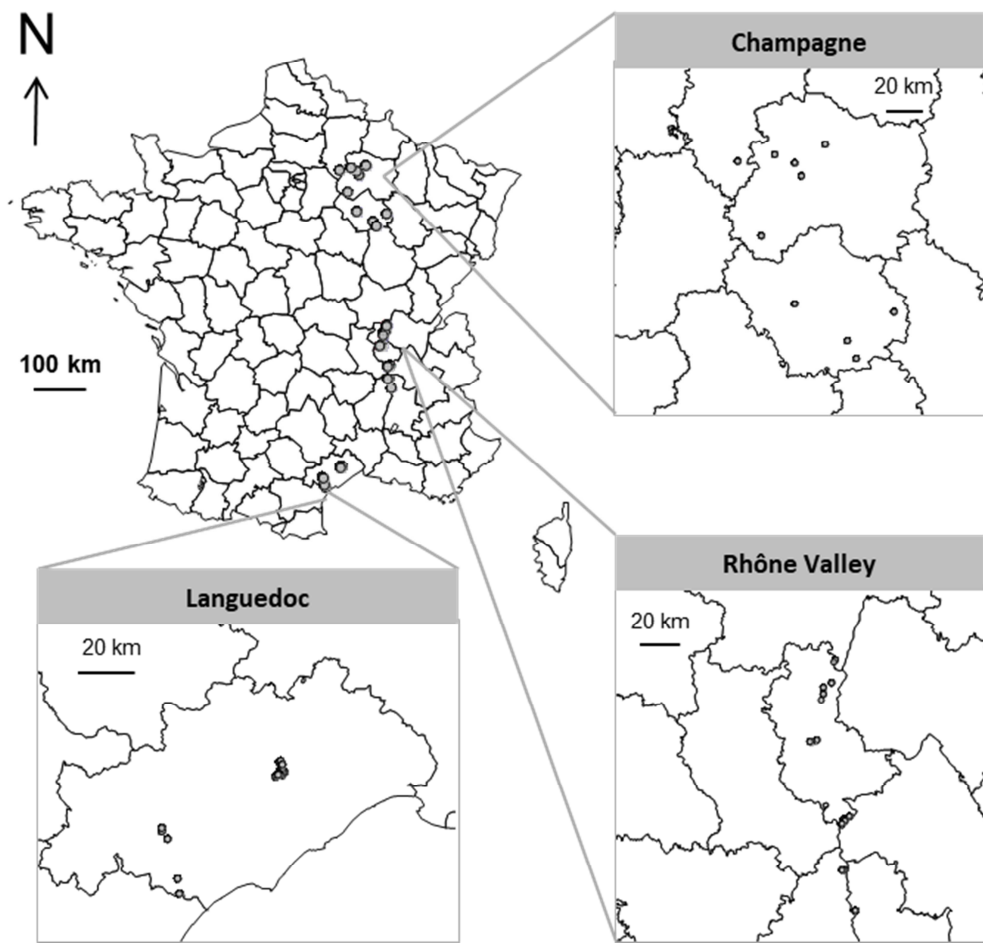


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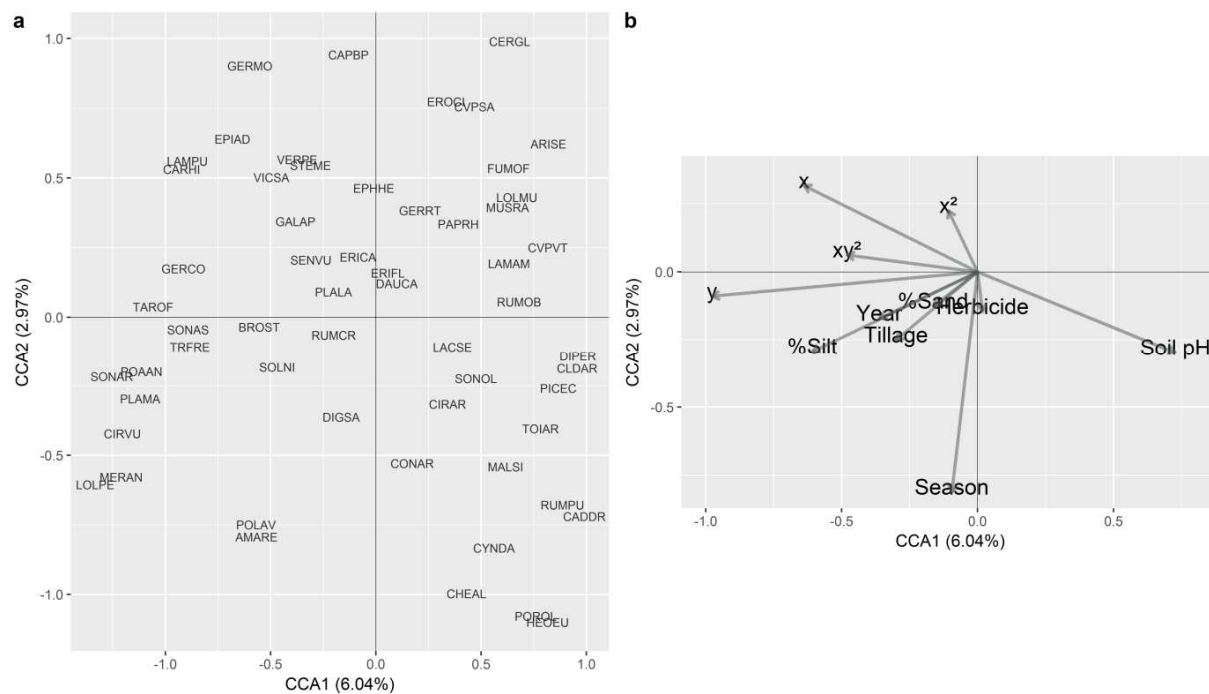


Figure 3. Ordination diagrams of the reduced CCA model containing a) the species (names coded with EPPO codes <https://gd.eppo.int/>) and b) the 11 significant explanatory variables. Only the species with the highest fit on the first two CCA axes are presented.

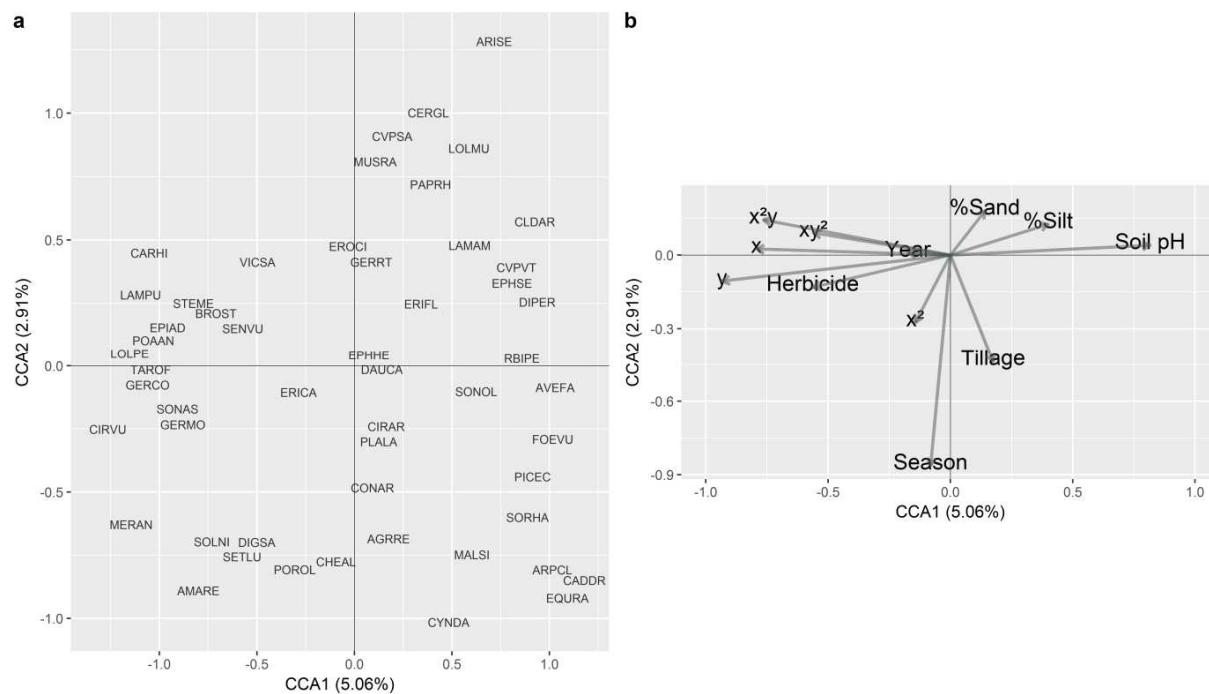


Figure 4. Mean species richness (S) and total abundance of vineyard plots in the inter- rows and the rows according to the main management practices : H = herbicides only, HT = combination of herbicides and soil tillage, T = soil tillage only, TM = combination of soil tillage and mowing (management practices 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.

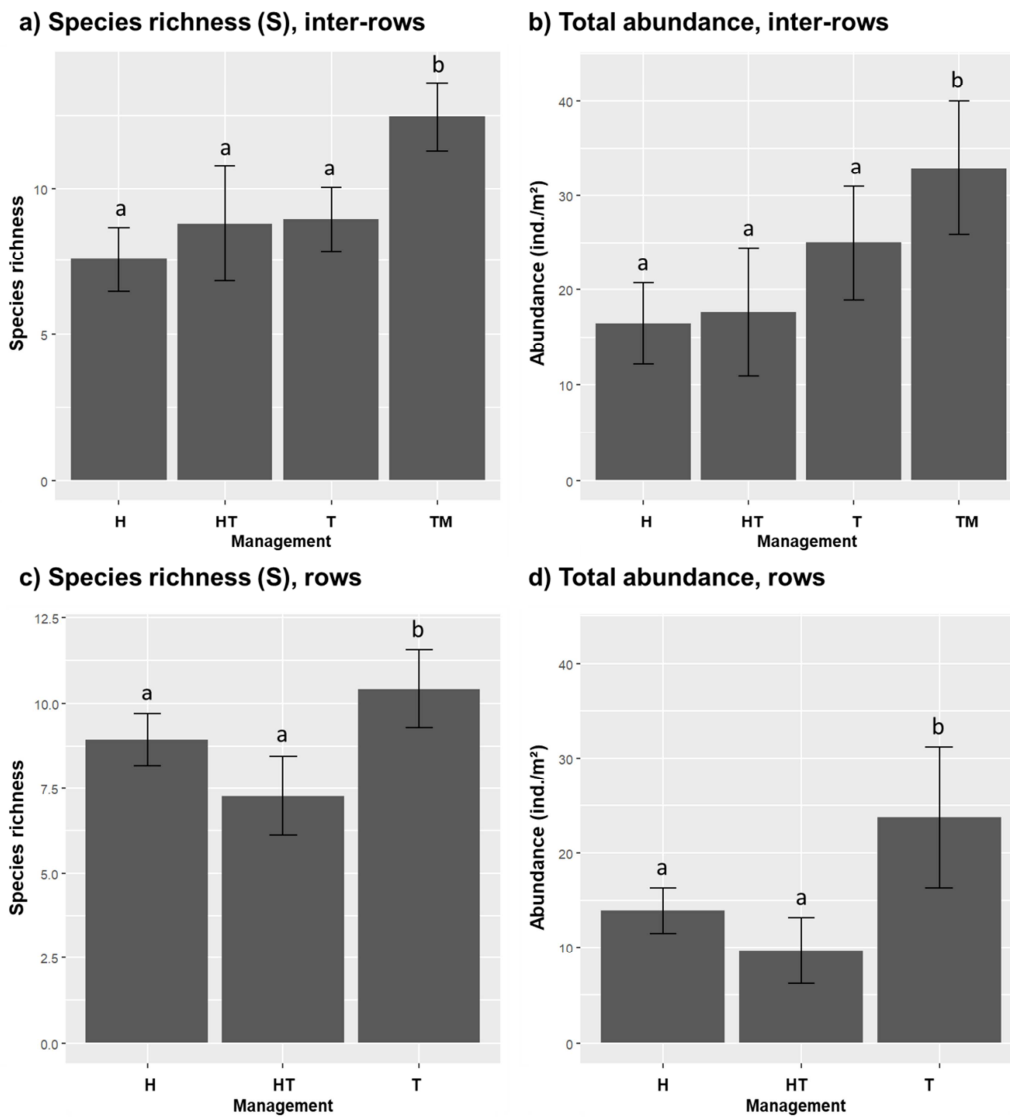
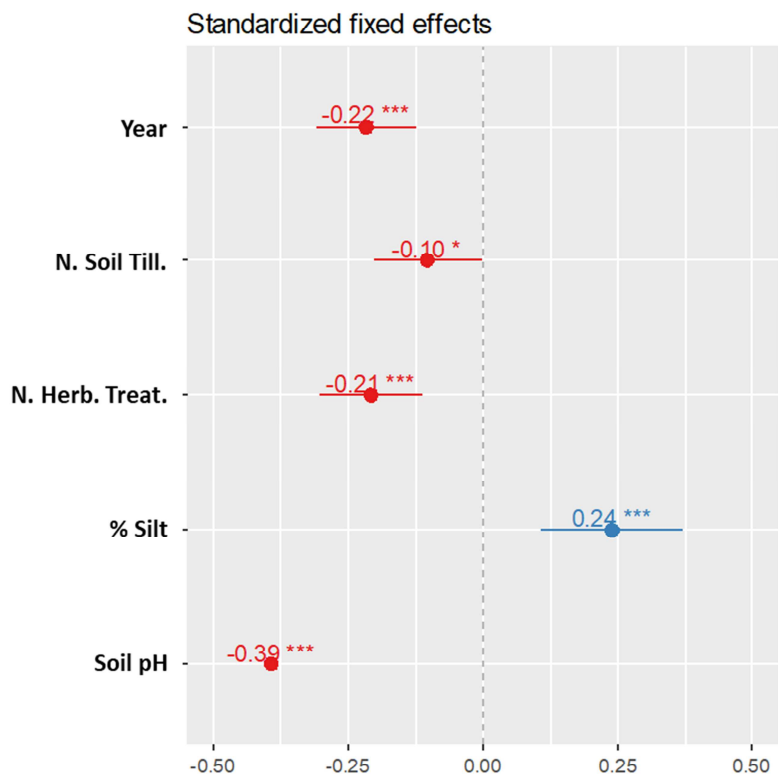


Figure 5. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's inter-rows

a) Species richness on vine's inter-rows



b) Species abundance on vine's inter-rows

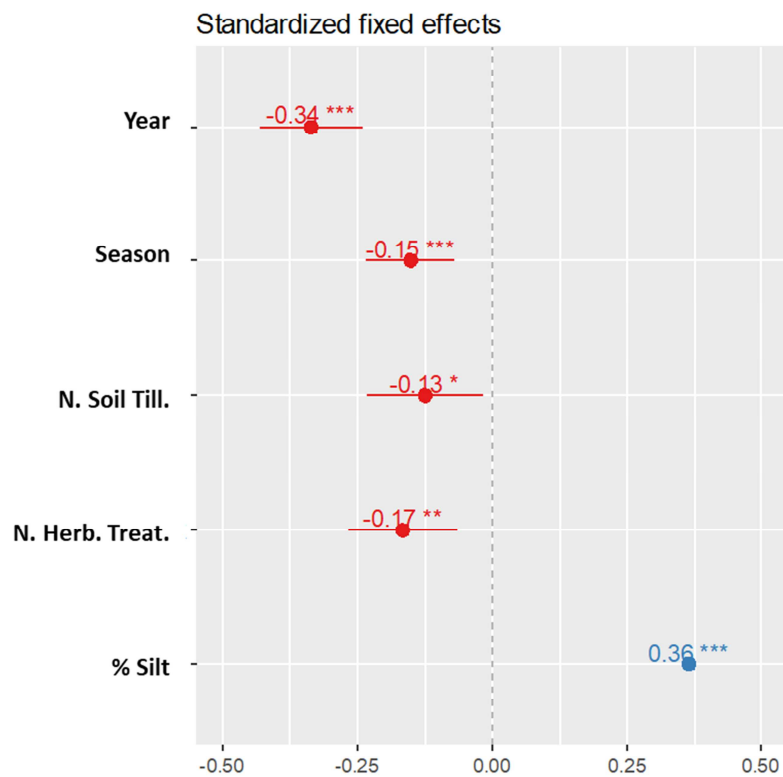
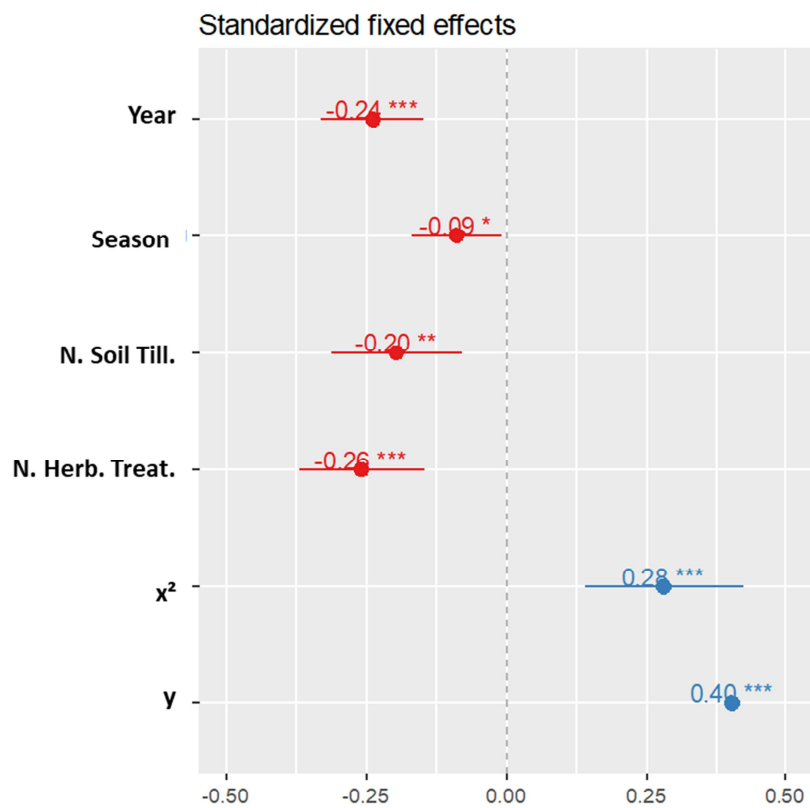


Figure 6. Standardized effects of the fixed variables of the reduced model explaining a) species richness and b) species abundance on the vine's rows

a) Species richness on vine's rows



b) Species abundance on vine's rows

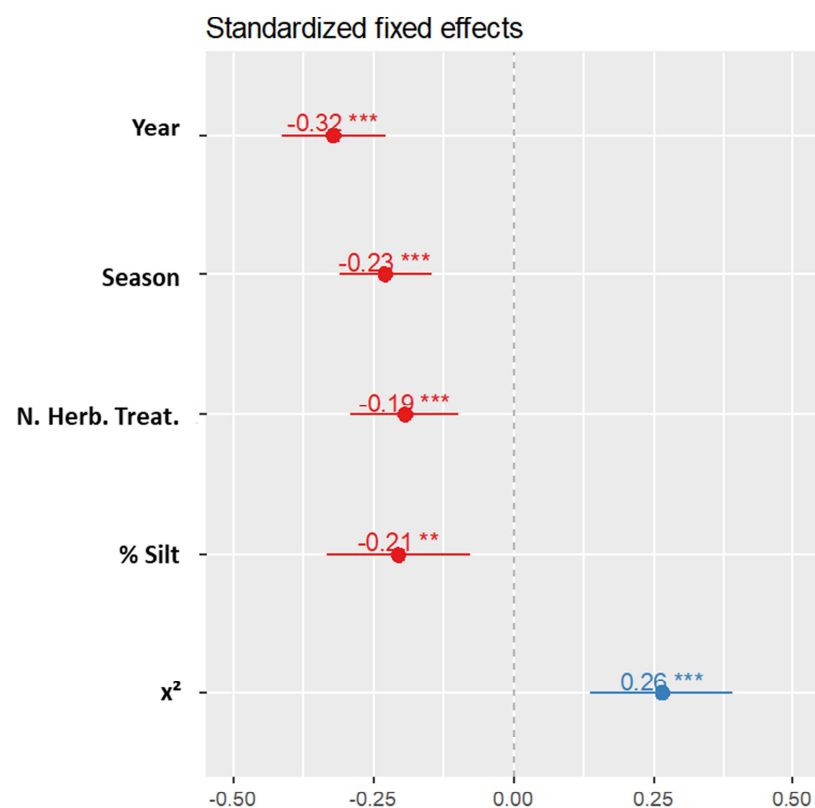


Table 1. Number of surveyed plots (#Plot) and floristic survey (#Surv.) by region and year. Season of floristic samples included late winter (W), spring (Sp), summer (Su) and autumn (A). Presence of a control plot (Cont.) without herbicide treatments is indicated.

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	
<i>(a) % of field with this Management Practices during the survey period</i>						
	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
<i>(b) Mean number of mowing, soil tillage or herbicides treatments per year¹</i>						
	R	IR	R	IR	R	IR
Number of mowing	0	<u>2</u>	0	<u>0.29</u>	0	<u>1.01</u>
Number of soil tillings	<i>1.43</i>	<u>2.39</u>	<i>1.21</i>	<u>1.78</u>	0.15	<u>1.32</u>
Number of herbicide treatments	<u>1.36</u>	0.57	<u>1.03</u>	0.85	<u>1.23</u>	0.39
<i>(c) % of surveys (plot x year) with this (combination of) management practices²</i>						
	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

¹Bold 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.

²Proportions 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, 1 st) – 319 (November, 15 th)
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		
<i>Management intensity</i>		
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
<i>Management type</i>		
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 ² y	-	-	-	-	-	-	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
<i>Heliotropium europaeum</i>	-1.294	0.057	<i>Poa annua</i>	-0.765	0.129	<i>Calendula arvensis</i>	-0.556	0.029	<i>Lepidium draba</i>	-0.558	0.011
<i>Digitaria sanguinalis</i>	-1.186	0.076	<i>Sonchus arvensis</i>	-0.622	0.023	<i>Malva sylvestris</i>	-0.468	0.027	<i>Rumex pulcher</i>	-0.307	0.013
<i>Portulaca oleracea</i>	-1.173	0.058	<i>Mercurialis annua</i>	-0.592	0.026	<i>Sonchus oleraceus</i>	-0.274	0.017	<i>Trifolium repens</i>	-0.175	0.022
<i>Chenopodium album</i>	-0.897	0.099	<i>Amaranthus retroflexus</i>	-0.587	0.022	<i>Diploaxis erucoides</i>	-0.232	0.016	<i>Torilis arvensis</i>	-0.105	0.009
<i>Convolvulus arvensis</i>	-0.534	0.080	<i>Galium aparine</i>	-0.564	0.020	<i>Erigeron canadensis</i>	0.301	0.017	<i>Crepis sancta</i>	0.000	0.011
<i>Erodium cicutarium</i>	0.463	0.044	<i>Cardamine hirsuta</i>	-0.383	0.018	<i>Taraxacum officinale</i>	0.312	0.029	<i>Lactuca serriola</i>	0.030	0.015
<i>Cerastium glomeratum</i>	0.667	0.052	<i>Diploaxis erucoides</i>	0.228	0.015	<i>Erodium cicutarium</i>	0.400	0.033	<i>Convolvulus arvensis</i>	0.048	0.015
<i>Crepis sancta</i>	0.689	0.132	<i>Erodium cicutarium</i>	0.360	0.026	<i>Geranium molle</i>	0.544	0.021	<i>Calendula arvensis</i>	0.169	0.008
<i>Cardamine hirsuta</i>	0.794	0.075	<i>Daucus carota</i>	0.485	0.017	<i>Portulaca oleracea</i>	0.721	0.022	<i>Galium aparine</i>	0.364	0.011
<i>Capsella bursa-pastoris</i>	0.833	0.059	<i>Euphorbia helioscopia</i>	0.507	0.017	<i>Vicia sativa</i>	0.871	0.052	<i>Cerastium glomeratum</i>	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
<i>Setaria pumila</i>	-1.024	0.064	<i>Cirsium vulgare</i>	-1.159	0.060	<i>Polygonum aviculare</i>	-0.619	0.023	<i>Muscari comosum</i>	-0.512	0.037
<i>Digitaria sanguinalis</i>	-0.983	0.052	<i>Sonchus arvensis</i>	-1.020	0.040	<i>Erigeron sumatrensis</i>	-0.511	0.015	<i>Calendula arvensis</i>	-0.453	0.019
<i>Chenopodium album</i>	-0.874	0.062	<i>Mercurialis annua</i>	-1.003	0.072	<i>Daucus carota</i>	-0.468	0.027	<i>Mercurialis annua</i>	-0.410	0.015
<i>Solanum nigrum</i>	-0.766	0.054	<i>Geranium columbinum</i>	-0.556	0.029	<i>Galium aparine</i>	-0.450	0.021	<i>Polygonum aviculare</i>	-0.381	0.016
<i>Convolvulus arvensis</i>	-0.494	0.094	<i>Poa annua</i>	-0.547	0.039	<i>Cerastium glomeratum</i>	-0.432	0.022	<i>Setaria pumila</i>	-0.362	0.015
<i>Fumaria officinalis</i>	0.651	0.064	<i>Anisantha sterilis</i>	-0.500	0.026	<i>Plantago lanceolata</i>	0.467	0.037	<i>Lactuca serriola</i>	0.207	0.015
<i>Lolium multiflorum</i>	0.654	0.040	<i>Senecio vulgaris</i>	-0.287	0.033	<i>Avena fatua</i>	0.633	0.033	<i>Malva sylvestris</i>	0.284	0.017
<i>Crepis sancta</i>	0.664	0.099	<i>Helminthotheca echioides</i>	0.467	0.025	<i>Equisetum ramosissimum</i>	0.703	0.043	<i>Torilis arvensis</i>	0.518	0.024
<i>Lamium purpureum</i>	0.679	0.050	<i>Rumex crispus</i>	0.594	0.027	<i>Lepidium draba</i>	1.109	0.091	<i>Sonchus arvensis</i>	0.591	0.032
<i>Cardamine hirsuta</i>	0.849	0.082	<i>Equisetum ramosissimum</i>	0.698	0.043	<i>Rumex crispus</i>	1.166	0.106	<i>Sorghum halepense</i>	0.715	0.036