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Marie-Charlotte Bopp, Elena Kazakou, Aurélie Metay, Jacques Maillet,
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4 Climate and management changes drove more stress-tolerant and less competitive plant
5 communities in 40 years

6 **Authors**

7 Marie-Charlotte Bopp^{1*}, Elena Kazakou¹, Aurélie Metay², Jacques Maillet³, Marie-Claude
8 Quidoz¹, Léa Genty^{2,4}, Guillaume Fried⁵

9 **Author names and affiliations**

10 ¹CEFE, Univ Montpellier, CNRS, EPHE, IRD, Institut Agro, Montpellier, France

11 ²UMR ABSys, Institut Agro, Inrae, Cirad, CIHEAM-IAMM, Univ Montpellier, 2 Place Pierre
12 Viala, 34060 Montpellier, France

13 ³Institut Agro, Inrae, Cirad, CIHEAM-IAMM, Univ Montpellier, 2 Place Pierre Viala, 34060
14 Montpellier, France

15 ⁴CIRAD, UMR ABSys, F-34398 Montpellier, France

16 ⁵Anses, Laboratoire de la Santé des Végétaux, Unité Entomologie et Plantes invasives, 34988
17 Montferrier-sur-Lez, France

18 **Corresponding author**

19 Marie-Charlotte Bopp: marie-charlotte.bopp@outlook.fr

20 **Open Research statement**

21 Data will be available in InDoRES once the manuscript will be accepted

22 (<https://www.indores.fr/>).

23 **Keywords**

24 Climate change ; CSR strategies ; Mediterranean vineyards ; trait-based approach ; weed

25 community ; weed management change ; 40-years temporal changes.

26

27

28 **Abstract**

29 Spontaneous plant communities have undergone considerable constraints due to human-mediated
30 changes. Understanding how plant communities are shifting in response to land management and
31 climate changes is necessary to predict future ecosystem functioning and improve the resilience
32 of managed ecosystems, such as agroecosystems. Using Mediterranean weed communities as
33 models of managed plant communities in a climate change hotspot, we quantified to which extent
34 they have shifted from the 1980s to the 2020s in response to climate and management changes in
35 vineyards. In four decades, the annual range of temperatures (*i.e.* the difference between the
36 warmest month's and the coldest month's mean temperatures) increased by 1.2°C and the summer
37 temperatures by 2°C. Weed management diversified over time with the adoption of mowing that
38 replaced the chemical weeding of inter-rows. Current weed communities were 41% more
39 abundant, 24% more diverse and with a less even distribution of abundance across species than
40 the 1980s communities at the vineyard level. Modern communities were composed of more
41 annual species (57% of annual species in the 1980s versus 80% in the 2020s) with lower lateral
42 spreadability and seed mass and were composed of fewer C4 species. They had higher
43 community-weighted specific leaf area, higher leaf dry matter content and lower leaf area than
44 1980s weed communities. At the community level, the onset of flowering was earlier and the
45 duration of flowering was longer in the 2020s. Climate change induced more stress-tolerant
46 communities in the 2020s while the diversification of weed management practices over time
47 filtered less competitive communities. This study shows that plant communities are adapting to
48 climate change and that land management is a strong lever for action to model more diverse and
49 functional plant communities in the future.

50

51 INTRODUCTION

52 Spontaneous plant communities have undergone considerable constraints due to human-mediated
53 changes at global (*e.g.* climate change) and regional scales (*e.g.* land use change) (Inderjit et al.
54 2017). At the global scale, climate change results in higher temperatures, altered precipitation,
55 higher frequency of extreme weather events and increased level of CO₂ (Peters, Breitsameter, and
56 Gerowitt 2014). The Mediterranean area has been identified as a ‘climate change hotspot’,
57 exceeding global warming average rates by 20% and having reduced rainfall, especially in
58 summer (Ali et al. 2022). Consequently, climate change is expected to impact disproportionately
59 Mediterranean vegetation compared to other regions of the world (Newbold et al. 2020). The
60 projections of the effect of climate change on plant communities are severe: decreased species
61 richness, reduction of the species range, shifts toward a higher proportion of annual species in
62 communities and a lower proportion of forbs (Pfeifer & Meister et al. 2016; Sala et al. 2000).
63 These changes in plant composition can ultimately alter many ecosystem processes (Cardinale et
64 al. 2012). This changing global filter also interacts with regional filters like human management
65 (Bourgeois et al. 2021) which have become more pronounced during the last decades. In the last
66 50 years, agriculture intensification including herbicides and mineral fertilizers uses has exerted
67 strong selection pressures on spontaneous plant communities, favouring communities adapted to
68 a high level of disturbance and resources (Bourgeois et al. 2019). As a result of this more
69 intensive weed management, the diversity of weed communities has also dramatically decreased
70 in arable lands (Fried, Chauvel, and Reboud 2009; Cirujeda, Aibar, and Zaragoza 2011; Fried,
71 Dessaint, and Reboud 2016; Storkey et al. 2011; 2021).

72 In agroecosystems, the temporal changes in plant communities were mostly described in
73 annual cropping systems while few studies have investigated spontaneous flora shifts in less

74 disturbed systems like perennial cropping systems. We assume that Mediterranean vineyard weed
75 communities are particularly relevant models to study flora shifts because the agricultural
76 practices of vineyards strongly evolved from the late 1970s to nowadays. At the end of the 1970s,
77 herbicides started to be widely applied on both the rows and the inter-rows of vines (*i.e.* the free
78 space between the rows of vines) (Maillet 1981). This constituted an abrupt change in
79 environmental conditions resulting in drastic changes in weed communities (Maillet 1992). In the
80 2000s, the awareness of the detrimental effects of herbicides on the environment (*e.g.* water
81 quality) forced farmers to limit their use. Superficial tillage and mowing gradually replaced
82 herbicide use in the inter-rows, leading to more integrated weed management (Fernández-Mena
83 et al. 2021). In addition, regulations are increasingly restricting the use of herbicides, with, for
84 example, a ban on the use of glyphosate in the inter-rows of French vineyards from 2021
85 (ANSES 2020). However, chemical weeding of the rows is still possible and frequent in French
86 Mediterranean vineyards (Bopp, Fried, et al. 2022).

87 Trait-based approaches provide a relevant framework to better understand how weed
88 communities shift in response to climate and management changes (Richner et al. 2015).
89 Functional trait values at the community level, also known as ‘functional markers’ (Garnier et al.
90 2004), respond to environmental filtering (*e.g.* climate change) (Lavorel and Garnier 2002) and
91 anthropogenic drivers (*e.g.* agricultural practices) (Booth and Swanton 2002; Navas 2012;
92 Damour, Navas, and Garnier 2018). This approach assumes that only certain species with specific
93 trait values will persist within communities in particular climate and management conditions.
94 Synchronic Mediterranean studies of trait patterns along aridity gradients in natural environments
95 suggested that climate change filter communities with a more resource-conservative strategy:
96 communities with small species, low leaf area and specific leaf area (SLA) and populations with

97 short flowering duration (Costa-Saura et al. 2016; Nunes et al. 2017; de la Riva et al. 2018).
98 Moreover, high temperatures and frequent drought would favour C4 weed species (Korres et al.
99 2016), late-emerging and thermophilic species (Peters, Breitsameter, and Gerowitt 2014) while
100 rising CO₂ atmospheric pressure is expected to favour C3 species. Thus, the impact of climate
101 change on photosynthetic pathways is not entirely clear (Peters, Breitsameter, and Gerowitt
102 2014). Yet, few studies have revealed how climate change might modify plant communities using
103 diachronic approaches (Feeley et al. 2020; Harrison, Spasojevic, and Li 2020).

104 Weed management practices can be considered as anthropogenic disturbances and can be
105 classified according to their intensity and frequency (Kazakou et al. 2016; Gaba et al. 2014). For
106 instance, chemical weeding and tillage represent both high-intensity disturbances as they
107 destroyed the whole aboveground biomass (Kazakou et al. 2016). In contrast, mowing might be
108 considered a lower-intensity disturbance as this practice removes the aboveground biomass
109 partially (MacLaren, Bennett, and Dehnen-Schmutz 2019). Recent synchronic studies (*i.e.*
110 comparing simultaneously vineyards with different managements) demonstrated the strong
111 filtering effects of management on weed communities in vineyards (Kazakou et al. 2016;
112 MacLaren, Bennett, and Dehnen-Schmutz 2019). More precisely, mowing favoured more weed
113 communities composed of conservative and competitive species, *i.e.* with more perennials, higher
114 seed mass, higher stature, lower specific leaf area (SLA) and higher leaf dry matter content
115 (LDMC) than communities managed with other practices like tillage (Hall et al. 2020; Mainardis
116 et al. 2020; Kazakou et al. 2016; Guerra et al. 2021; Bopp, Kazakou, et al. 2022; Fried et al.
117 2022). In contrast, tillage and chemical weeding favoured communities composed of acquisitive
118 species, *i.e.* annual species with high SLA and low LDMC and late-flowering populations (Hall
119 et al. 2020; Bopp, Kazakou, et al. 2022; Fried et al. 2022). However, herbicides were shown to
120 favour contrasted life forms in weed communities: both annual and some perennial species (*e.g.*

121 geophytes) (Hall et al., 2020). The CSR scheme of Grime (1977) is an integrative approach to
122 studying adaptative strategies that species use to cope with two constraints: (i) stress related to
123 lower resource availability (*e.g.* water stress related to climate change in the Mediterranean area)
124 and (ii) disturbance related to the sudden destruction of biomass (*e.g.* weed management practice
125 as tillage, mowing, chemical weeding). The CSR scheme describes three main species strategies:
126 (i) stress tolerators (S) in resource-poor habitats with low disturbance, (ii) ruderals (R) in
127 resource-rich and highly disturbed environments (*e.g.* agroecosystems) and (iii) competitors (C)
128 in highly productive habitats with low-stress intensity and disturbance. If weed species are mostly
129 ruderals as cultivated habitats are by definition regularly disturbed by tillage (Mahaut et al. 2020;
130 Bourgeois et al. 2019), a recent study demonstrated that the proportion of CSR strategies in weed
131 communities changed according to the weed management used (Fried et al. 2022). For instance,
132 mowing favoured communities with more competitive strategies while tillage favoured species
133 with more ruderal strategies. Climate change might also modify the relative proportion of
134 species's CSR strategies within the communities over time (MacLaren et al. 2020). For instance,
135 under climate change, weed species with stress tolerator strategies are more likely to occur
136 (Korres et al. 2016). If recent synchronic studies exist in weed functional response to
137 management (*e.g.* MacLaren et al. 2019, Hall et al. 2020) or to climate (Bopp, Kazakou, et al.
138 2022), no study, to our knowledge, has yet been conducted on weed community functional
139 changes over time in vineyards.

140 In this study, we quantified how climate and management changes have shifted weed
141 communities from the 1980s to the 2020s, using a historic network of 40 Mediterranean
142 vineyards in South France. First, we assessed climate change intensity and characterise changes
143 in weed management practices in the vineyard network. Then, we described shifts in taxonomic
144 and functional weed community structures after four decades using 374 floristic surveys that

145 were performed during two years at each period (1978, 1979, 2020, 2021) and at 3 seasons
146 (March, June, October). Finally, we tested if climate conditions and weed management practices
147 drove changes in weed community structure between the 1980s and the 2020s. We hypothesised
148 that climate change would favour species with more water-conservative traits (*e.g.* C4
149 metabolism, small leaf area, high LDMC) and stress-tolerant strategies. Moreover, we expected
150 that the decrease in herbicide use replaced by mowing would favour more conservative and
151 competitive strategies.

152

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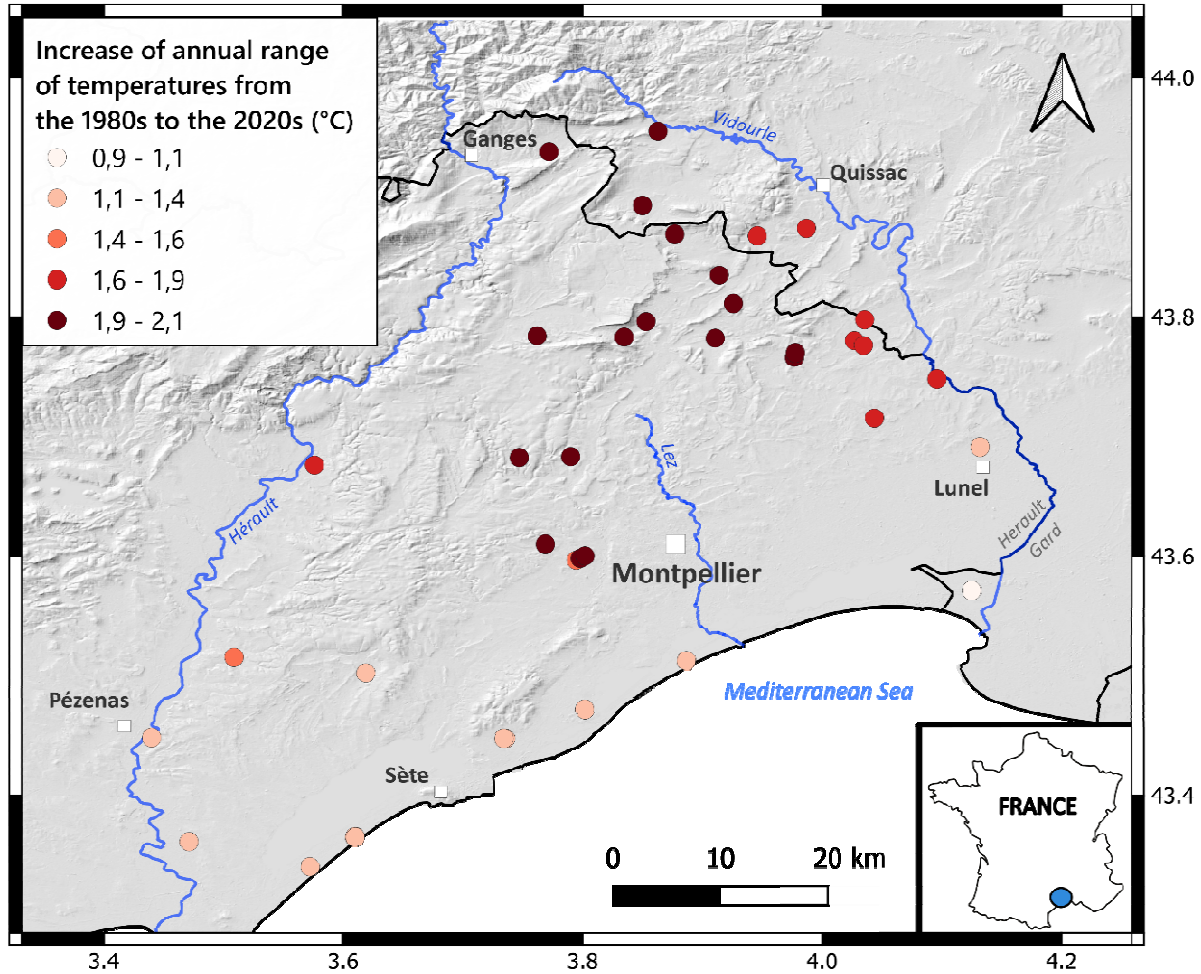
154 MATERIAL AND METHODS

155 1. Climate, soil and weed management characterisation of the historical vineyard 156 network

157 The network was composed of 40 vineyards located around Montpellier, France (Figure 1). This
158 network was first set up in 1978 to study weed management effects on weed community
159 composition (Maillet 1981). The vineyards are located in a Mediterranean climate characterised
160 by warm temperatures (14°C mean annual temperatures on average from 1978 to 2021), irregular
161 rainfall (814 mm per year) and dry summers (88% of annual precipitation occurs during the other
162 seasons). Soil textures of vineyards varied along a North-East/South-West gradient determined
163 by the distance to the Mediterranean Sea: from sandy vineyards nearby the Sea to loamy and
164 clay/loamy soils in further northeast vineyards.

165 To characterise climate change, variables describing seasonal and annual climate were
166 extracted from the estimations obtained by the SAFRAN interpolation method (Analysis system
167 providing atmospheric information to the snow) on an 8 km × 8 km grid (Durand et al. 1993)
168 from 1971 to 2021. Eleven variables were selected: mean seasonal temperatures and rainfall
169 (spring, summer, autumn and winter), growing season length (GSL) (*i.e.* the number of days in a
170 year with daily mean temperature above 5°C during at least 6 consecutive days), numbers of frost
171 days and annual range of temperatures (*i.e.* the difference between the warmest month's and the
172 coldest month's mean temperatures), and were averaged over 5 different decades from 1971 to
173 2021 (1971-1980 ; 1981-1990 ; 1991-2000 ; 2001-2010 ; 2011-2021). Due to the SAFRAN grid,
174 31 neighbouring vineyards on 40 shared the same climate data at least with another vineyard: 20
175 squares of 8x8 km² with different climate data were used for the 40 vineyards of the network.

176 To characterise changes in weed management practices of the rows and the inter-rows
177 from 1978 to 2021, we conducted two interviews in 2020 and 2021 with each farmer of the
178 network (see Appendix 3: Section S1). We considered the five following binary practice
179 variables: (i) chemical weeding of rows, (ii) chemical weeding of inter-rows, (iii) tillage of rows,
180 (iv) tillage of inter-rows and (v) mowing of inter-row. Each variable had two possible values: 0,
181 not applied; 1, applied. To define the trajectory of the weed management practices of each
182 vineyard, we used the values of these five variables over five different periods: 1978-1979 (the
183 initial weed management practices) ; 1980-1990 ; 1991-2000 ; 2001-2010 and 2011-2021 (the
184 final weed management practices).



185

186 Figure 1 Geographical distribution of the increase of annual range of temperatures from the
187 1980s to the 2020s experienced by the 40 vineyards of the network, Montpellier, France. Each
188 dot is a vineyard and its colour represents the extent of the increase in the annual range of
189 temperatures (from light red for low increases to dark red for high increases). The dark lines
190 represent the department's outlines. The blue lines represent the main rivers of the region. The
191 values displayed on the frame surrounding the map are the latitudinal and longitudinal
192 coordinates.

193

194 **2. Weed community composition in the 1980s and the 2020s**

195 Weed community composition was determined in 1978 and 1979 (as ‘1980s communities’
196 hereafter) (Maillet 1981) and in 2020 and 2021 (as ‘2020s communities’) at 3 different seasons
197 (late winter, early summer and autumn) (Appendix S1: Figure S1). In total, the dataset was
198 composed of 374 floristic surveys (for more details, see Appendix S1: Figure S1). To compare
199 the floristic compositions over the two periods, we applied the same method of floristic surveys.
200 In each vineyard, a rectangular area of 400 m² (40m x 10m) was delimited (4 inter-rows and 3
201 rows of the same length). To estimate species abundance, we used five abundance classes
202 developed in Barralis (1976): ‘1’, less than 1 individual/m²; ‘2’, 1–2 individuals/m²; ‘3’, 3–20
203 individuals/m²; ‘4’, 21–50 individuals/m²; ‘5’, more than 50 individuals/m². We transformed
204 these scores into a quantitative scaling using the median of the range of each density class as
205 followed: ‘1’, 0.5 individual/m²; ‘2’, 1.5 individuals/m²; ‘3’, 11.5 individuals/m²; ‘4’, 35.5
206 individuals/m²; ‘5’, 75 individuals/m². A list of species and distinct abundance scores were noted
207 at the plot level. To control the ‘observer effect’, we conducted several floristic surveys in 2020
208 with Jacques Maillet, who conducted the floristic surveys in the 1980s. No major biases were
209 observed during these floristic surveys. For each community, we computed the richness, the
210 abundance (*i.e.* the sum of the density of each species), the Shannon diversity index and Pielou’s
211 evenness index which is the ratio between the Shannon index and the logarithm of the community
212 richness (Pielou 1966).

213 **3. Functional properties of the 1980s and 2020s weed communities**

214 Seven plant traits, two phenological population-level traits and four Ellenberg indices were
215 selected to capture plant responses to climate change and weed management changes. Three traits
216 of the Leaf-Height-Seed (LHS) strategy scheme were selected (Westoby, 1998): 1) specific leaf

217 area (SLA, $\text{m}^2 \cdot \text{kg}^{-1}$) related to the speed of resources acquisition (Wright et al., 2004), 2)
218 maximum height (m) related to light and nutrient acquisition (Westoby et al., 2002), 3) seed mass
219 (g) which represents the “colonisation-competition” trade-off (Moles and Westoby, 2006). Leaf
220 area (m^2) was also selected as a good *proxy* for the competitive abilities of plants and lateral
221 spread as a response trait to disturbance. This qualitative trait represents species’ abilities to
222 develop horizontally (species with rhizomes or forming tussocks); it is rated as followed: “1”,
223 therophytes ; “2”, perennials with compact unbranched rhizomes or forming small tussocks (less
224 than 100 mm in diameter) ; “3”, perennials with a rhizomatous system or tussocks reaching from
225 100 to 250 mm ; “4”, perennials reaching a diameter of 251 to 1000 mm. Leaf Dry Matter
226 Content (*i.e.* the ratio between leaf dry mass and leaf fresh mass) was selected as a *proxy* for
227 plant investment in leaf structure. Photosynthesis pathways (C3/C4) were assessed to identify the
228 species with water-saving photosynthesis (Pyankov et al. 2010). Phenology was characterised by
229 the months of flowering onset and the number of months of flowering determined at the
230 population level for each species. Species resource requirements were characterised through four
231 Ellenberg indices: light (EIV_L), temperature (EIV_T), soil moisture (EIV_F) and nitrogen
232 (EIV_N). Raunkiær plant life forms were included.

233 Leaf area, SLA and LDMC were measured on the weed species present in the 2020s
234 communities (8 individuals per species). The other traits were extracted from different databases:
235 Seed Information Database for seed mass (Royal Botanic Gardens Kew 2021), *Flora Gallica* for
236 maximum height (Tison and De Foucault 2014), lateral spread from Hodgson et al. (1995)
237 supplemented by expert opinion (G. Fried, pers. com.), Baseflor for flowering onset, duration of
238 flowering and the four Ellenberg indices (Julve 1998). Flowering onset and duration of flowering
239 are quantified at the population level and not at the individual level (*i.e.*, a long flowering

240 duration does not mean that individuals of that species can flower during a long period but that
241 different individuals of that species cover together a long period of flowering). Photosynthetic
242 pathways were extracted from Pyankov et al. (2010).

243 To scale up the trait values from the species level to the community level, we calculated
244 Community Weighted Means (CWM, *i.e.* the average of the trait values of species present in a
245 community, weighted by their relative abundances) (Garnier et al. 2004) using at least 80% of the
246 most abundant species of the weed communities in the calculation (Mass ratio hypothesis, (Grime
247 1998)). We calculated median values for lateral spread and the percentage of C4 species'
248 abundance within the communities. Based on the CWM of SLA, LDMC and leaf area, we
249 calculated the competitiveness (C), stress-tolerance (S) and ruderal (R) scores following Pierce et
250 al. (2017) and Li and Shipley (2017).

251 **4. Data analyses**

252 **a) Description of climate, weed management and weed community functional structure** 253 **using multivariate analyses**

254 Multivariate analyses were performed to characterise climate and weed management changes
255 per decade from the 1980s to the 2020s (1980s, 1990s, 2000s, 2010s and 2020s) (see Appendix
256 S3: Section S2). Four categories of the 2020s weed management were defined using a Principal
257 Component Analysis (PCA) and hierarchical clustering (see Appendix S1: Figure S2, Appendix
258 S3: Section S3). Cluster 'Chem' gathers four vineyards with chemical weeding of both rows and
259 inter-rows. Cluster 'Till.IR.Chem.R' regroups 19 vineyards with tilled inter-rows and chemically
260 weeded rows. Cluster 'Mow.IR.Till.R' gathers 11 vineyards with mowed inter-rows and tilled
261 rows. Cluster 'Till' groups six vineyards with tilled rows and inter-rows. A PCA was also
262 performed on the CWM of the 13 traits of the 1980s and 2020s communities. To select a

263 parsimonious number of dimensions which represents well the functional space, we used the
264 elbow inflexion point method on the Area Under the Curve (AUC) and the Mean Absolute
265 Deviation (MAD) following Mouillot et al. (2021).

266 **b) Comparison of structure and composition of the 1980s and 2020s weed communities**

267 Two different datasets were used for data analyses (Appendix S1: Figure S1). The first one is
268 the ‘full dataset’ composed the 374 floristic surveys from the 1980s and the 2020s. This dataset
269 was used to test the significance of the difference in means of taxonomic indices (abundance,
270 richness, Shannon, Pielou), Raunkiær plant life forms, CWM and CSR scores over time. Using
271 the full dataset (n=374), we fitted linear mixed models with the period (the 1980s/2020s) as a
272 fixed effect and the season (March/June/October), the year (1978, 1979, 2020, 2021) and plot
273 identity as random effects. An ANOVA was performed on these models to test fixed effect
274 significance. Post-hoc Tukey and Wilcoxon tests were then computed to assess the direction of
275 the changes in functional properties of weed communities from the 1980s to the 2020s.
276 Moreover, the changes in abundance and frequency of species over time were quantified using
277 indices of relative changes following this formula: $(\text{Indice}_{2020s} - \text{Indice}_{1980s}) / (\text{Indice}_{2020s} +$
278 $\text{Indice}_{1980s})$. From these indices, we identified (i) the species that increased in abundance and
279 frequency defined as the species with more than 0.75 of relative changes in abundance and
280 frequency, (ii) the species that decreased in abundance and frequency with less than -0.75 of
281 relative changes and (iii) the species that remained stable in abundance and frequency with
282 relative changes within the range of [-0.75 ; 0.75].

283

284 **c) Identification of the drivers of weed community structure shifts over time**

285 The second dataset was built to test whether climate and management changes explained the
286 changes in taxonomic and functional properties of weed communities (Appendix S1: Figure S1).
287 To build an ‘explaining’ dataset, we averaged the functional and taxonomic metrics over the two
288 years for each period: from 5 floristic surveys per period (*e.g.* for the 1980s, March 1978, 1979,
289 June 1978, 1979 and October 1979) to 3 floristic surveys per period (*e.g.* March 1980s, June
290 1980s, October 1980s). Then, each season of each period was comparable with the season of the
291 other period (*e.g.* March 1980s with March 2020s). This ‘explaining’ dataset was composed of
292 120 taxonomic and functional shifts of communities from the 1980s to the 2020s: 40 vineyard
293 community shifts x 3 seasons (Appendix S1: Figure S1). After removing missing data, the dataset
294 consisted of 108 functional shifts. We used two different ways of computing indexes of changes:
295 (i) for comparing coordinates of the CWM in the functional PCA, we computed the difference
296 between the coordinates in the 2020s and the coordinates in the 1980s for each selected axes of
297 the multivariate analysis (Appendix S2: Table S1) and (ii) for comparing ‘raw values’ of different
298 metrics (CWM, CSR scores, annual temperature range, abundance, richness, Shannon and Pielou
299 indices), we computed indices of relative changes using the following formula: $(\text{Indice}_{2020s} -$
300 $\text{Indice}_{1980s}) / (\text{Indice}_{2020s} + \text{Indice}_{1980s})$ (Appendix S2: Table S1).

301 We selected the climate and management drivers that explained most of the climate and
302 management changes over the four decades from the multivariate analyses based on climate and
303 management characteristics per decade. As a *proxy* for climate change, we selected the relative
304 changes in the annual T°C range between the 1980s and the 2020s (*i.e.* the difference between the
305 warmest months and the coldest month's mean temperatures). To describe weed management
306 trajectory, we used three variables: (i) the number of decades since herbicides were stopped, (ii)

307 the number of decades since mowing was used and (iii) the additional number of different
308 management practices applied at the plot level from the 1980s to the 2020s, as a *proxy* for the
309 trajectory toward more integrated weed management (*e.g.* if tillage was the only management
310 practice used in the 1980s and if mowing and tillage were used in 2020s, the value would be ‘1’
311 additional weed management practice applied). To describe current weed management, we
312 selected the categorical variable describing 2020s weed management practices with four different
313 groups (**‘Chem’**: vineyards with chemical weeding of both rows and inter-rows ;
314 **‘Till.IR.Chem.R’**: vineyards with tilled inter-rows and chemically weeded rows;
315 **‘Mow.IR.Till.R’**: vineyards with mowed inter-rows and tilled rows ; **‘Till’**: vineyards with tilled
316 rows and inter-rows) (Appendix S2: Table S1). Using the ‘explaining’ dataset (n=108), we fitted
317 linear mixed models to explain the shifts in CWM, taxonomic indices (abundance, richness,
318 Pielou, Shannon) and CSR scores over time by the selected drivers of climate and management
319 changes as fixed effects and with the season and plot identity as random effects. The selection of
320 models was done based on the corrected Akaike Information Criterion (AICc) with the *dredge*
321 function from the *MuMIn* R package (Burnham and Anderson 2002). All data analyses were
322 carried out using R version 4.1.1 (R Core Team 2021).

323 RESULTS

324 1. Climate and management changes from the 1980s to the 2020s

325 a) Climate change from the 1980s to the 2020s nearby Montpellier, France: the annual 326 range of temperature increased by 1.2°C

327 Over the two periods, seasonal climate variables (spring, summer, autumn, winter
328 temperature, spring, summer, autumn, winter rainfall, and the annual number of frost days) of the
329 vineyards were well explained by the first two PCA axes (84.7% of total variance) (Figure 2).
330 The first axis explained most of the climate variance (60.5%) and intra-network variations across
331 the vineyards from the same decades. This axis opposed vineyards located in warmer and drier
332 areas with longer growing season length, located near the coastline to vineyards located in areas
333 with higher rainfall, higher numbers of frost days and shorter growing season length, located in
334 the northeast of the network. This axis also represented a slight decrease in seasonal
335 precipitations over the decades (Appendix S1: Figure S3). The second axis described mostly
336 inter-decades variations of the climate conditions (24.2% of explained variance) (Figure 2,
337 Appendix S1: Figure S3). This axis was mainly driven by the annual range of temperatures (*i.e.*
338 the difference between the mean temperatures of the warmest month and the coldest month), the
339 summer mean temperature and the number of frost days. In 40 years, the annual range of
340 temperatures increased by 1.2°C (from 13.5°C averaged over the 1971-1980 decade to 14.7°C
341 averaged over the 2011-2021 decade). Moreover, summer mean temperatures have increased by
342 2°C in 40 years (21°C in the 1980s and 23°C in the 2020s) and spring temperatures by 1.4°C
343 (12°C in the 1980s to 13.4°C in the 2020s) (Table 1). The annual number of frost days doubled in
344 40 years: from 11 days in the 1980s to 23 in the 2020s (Table 1). Within the vineyard network,
345 the increase in the annual range of temperatures was heterogeneous and varied from an increase

346 of 0.9°C (vineyards located nearby the Mediterranean Sea) to an increase of 2.1°C (Northern
347 vineyards) (Figure 2).

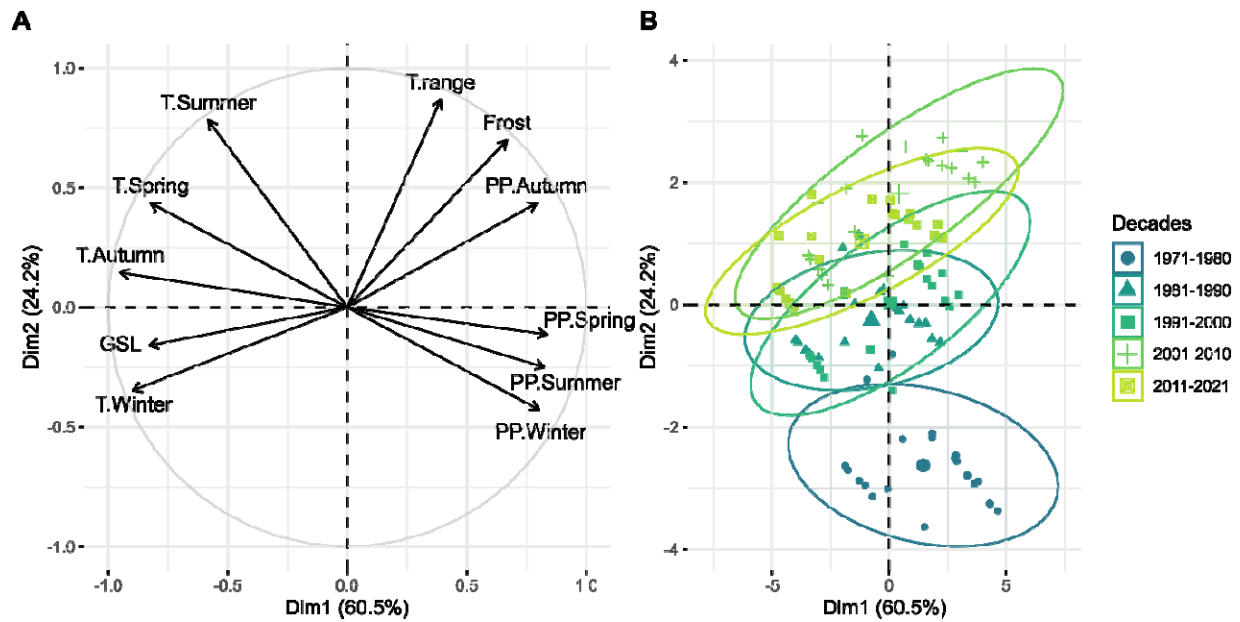


Figure 2 Climate change from the 1970s to the 2020s. **A)** Correlation circle of the climate variables on the first two axes of the climate PCA over the decades from the 1970s to the 2020s. **B)** Vineyard projection on the first two axes of the climate PCA for each decade from the 1970s to the 2020s. Each variable was averaged over the five studied decades: 1971-1980, 1981-1990, 1991-2000, 2001-2010, 2011-2021. T.Summer, mean summer temperature (°C) ; T.Spring, mean spring temperature (°C) ; T.Autumn, mean autumn temperature (°C) ; T.Winter, mean winter temperature (°C) ; PP.Spring, winter cumulated rainfall (mm) ; PP.Autumn, autumn cumulated rainfall (mm) ; PP.Winter, winter cumulated rainfall (mm) ; PP.Summer, summer cumulated rainfall (mm) ; T.range, annual temperature range (°C) ; Frost, number of frost days ; GSL, growing season length.

348

349 **b) Weed practice shifts in 40 years in Mediterranean vineyards: mowing**
350 **adoption from the 2000s**

351 The first two axes of the Principal Coordinates Analysis (PCoA) based on the weed
352 management practice variables of decades from the 1980s to the 2020s explained 72.2% of
353 the total variance (Figure 3). The first axis opposed weed management practices from
354 chemical weeding of rows ($\rho: -0.69, P < 0.001$) and inter-rows ($\rho: -0.77, P < 0.001$) to
355 tillage of rows ($\rho: 0.80, P < 0.001$) and inter-rows ($\rho: 0.64, P < 0.001$) and mowing of
356 inter-rows ($\rho: 0.48, P < 0.001$). The second axis discriminated the vineyards with low
357 numbers of weed management practices used at the plot level (1 or 2) from the ones with
358 more integrated weed management (*e.g.* 3 different weed management practices applied at the
359 plot level) (Figure 3). More precisely, this axis opposed vineyards with tilled rows ($\rho: -$
360 $0.32, P < 0.001$) and either chemical weeding or tillage of inter-rows to vineyards with a
361 mixed combination of tilled ($\rho: 0.51, P < 0.001$) and mowed inter-rows ($\rho: 0.69, P <$
362 0.001) and chemical weeding of rows ($\rho: 0.66, P < 0.001$). In the 1980s, farmers mostly
363 tilled and applied herbicides. The mowing practice appeared in the 2000s, diversifying and
364 increasing the number of weed management practices applied at the vineyard level. The
365 median weed management practice that farmers applied in the 2020s was inter-row tilling and
366 mowing and chemical weeding of rows (Figure 3). Thus, at the vineyard network level, the
367 weed management shift from the 1980s to the 2020s was characterised by (i) less use of
368 chemical weed control on the inter-rows and (ii) a combination of more weed management
369 practices at the plot level due to the adoption of mowing from the 2000s (Figure 3).

370

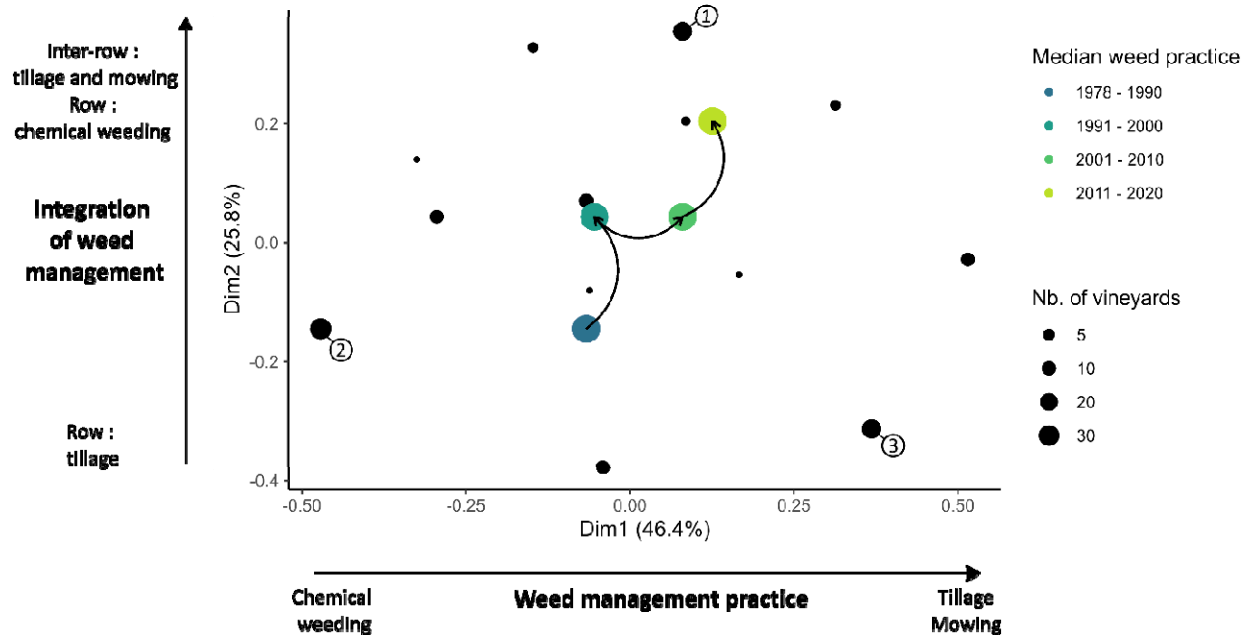


Figure 3 Changes in weed management practices from the 1980s to the 2020s in the Principal Coordinates Analysis (PCoA) space. Each dot represents a combination of weed practices at the plot level. The size of the black dots is proportional to the number of vineyards that share the same practice combination. The large coloured dots represent the median position of the vineyards of each decade in the PCoA space. The arrows illustrate the weed practice trajectory from the 1980s to the 2020s at the vineyard network scale. The first axis represents the weed management type used by the farmers. The second axis represents the number of weed practice types applied at the vineyard scale: from 1 practice type used (tillage of rows) to 3 practice types (tillage and mowing of inter-rows combined with chemically weeded rows). The vineyards located on position (1) in the practice PCoA are characterised by tillage and mowing of inter-rows and chemical weeding of the rows; the vineyards located on position (2) had chemically weeded rows and inter-rows; the vineyards located in position (3) have rows and inter-rows that are tilled. Nb. of vineyards, number of vineyards sharing the same weed management practices.

372 **2. Shifts in weed community structure from the 1980s to the 2020s**

373 In total, 436 species were found over the 374 floristic surveys of the two periods. At the
374 vineyard network scale, a similar number of species were identified 40 years apart: 320 species in
375 the 1980s and 319 species in the 2020s. At the vineyard scale, the mean species richness was
376 higher in the 2020s (34 species/community) than in the 1980s (26 species/community) (Figure 4).
377 Community density showed the same trend that species richness: 68 individual plant/m² were
378 found in the 2020s while 40 individual plant/m² were found in the 1980s. However, Shannon
379 diversity was not significantly different between the two periods (2.39 in the 2020s and 2.40 in
380 the 1980s) and the Pielou index was significantly lower in the 2020s (0.69 in the 2020s and 0.78
381 in the 1980s), demonstrating that the 2020s community were less equitable in abundance
382 (Appendix S1: Figure S4).

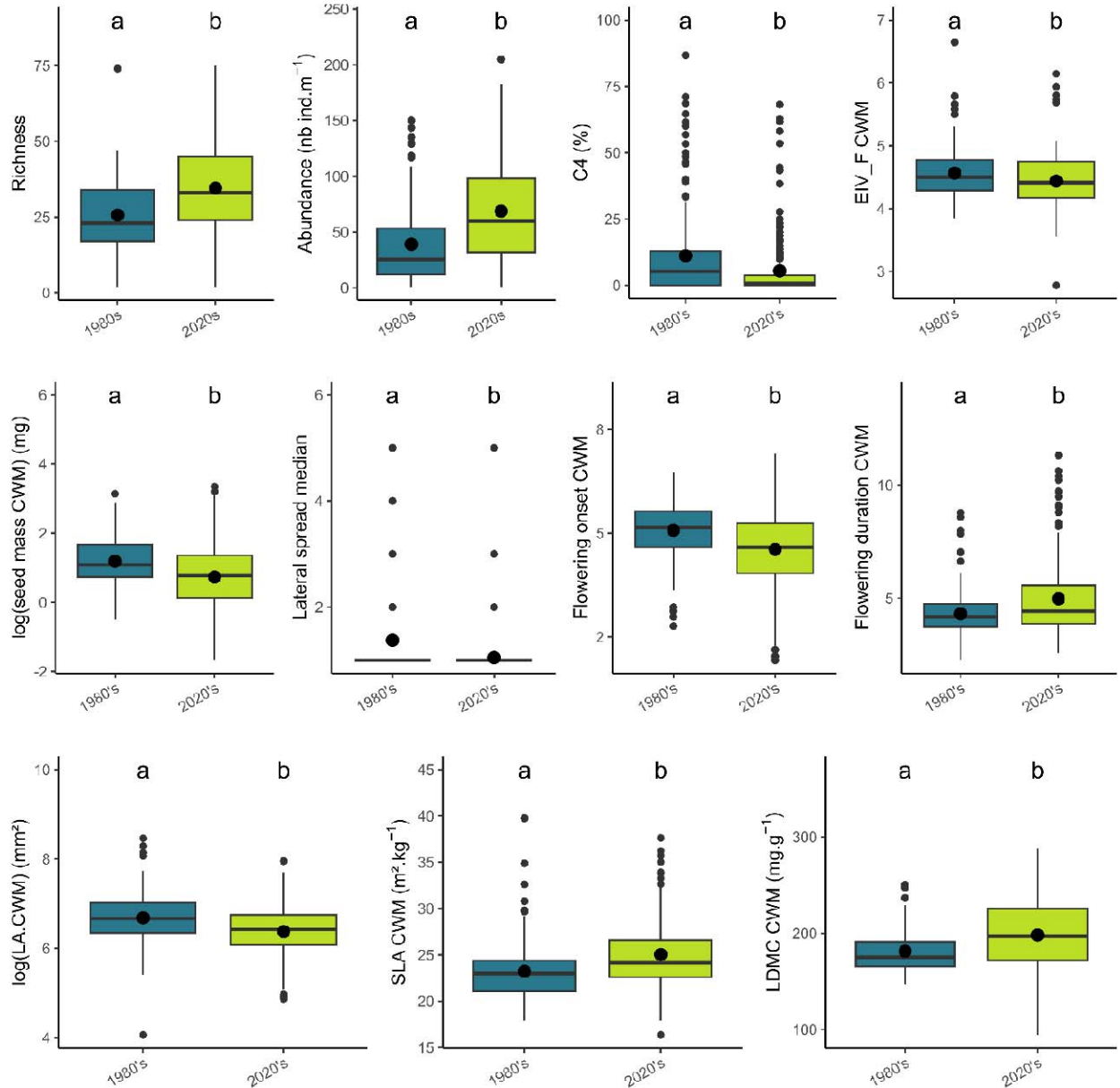


Figure 4 Significant changes in abundance, richness and functional properties of weed communities between the 1980s and the 2020s. CWM, Community Weighted Means ; EIV_F.CWM, Ellenberg indice for soil moisture ; LA, leaf area ; SLA, specific leaf area ; LDMC, leaf dry matter content. n = 374 floristic surveys

383

384

385 The 2020s weed communities were composed of more therophytes compared to the 1980s
386 communities (57% of the species in the 1980s compared to 80% in the 2020s) (Appendix S1:
387 Figure S5). In contrast, the 1980s communities were composed of more bulb geophytes (*e.g.*
388 *Allium vineale*) 7% of bulb geophytes composing 1980s communities while they represented 1%
389 of the weed communities in the 2020s. The 1980s weed communities were composed of more
390 rhizome geophytes (*e.g. Cynodon dactylon*) (10% in the 1980s versus 4% in the 2020s), more
391 biennial hemicryptophytes (*e.g. Chondrilla juncea*) (7% in the 1980s versus 5% in the 2020s),
392 more caespitose and erected hemicryptophytes (*e.g. Anthemis maritima*) (8% in the 1980s and 6%
393 in the 2020s) and more hemicryptophytes with stolons (*e.g. Convolvulus arvensis*) (9% in the
394 1980s versus 3% in the 2020s).

395 Out of 423 species, 73 species had a strong decrease in abundance from the 1980s to the
396 2020s (more than 75%) while 116 species had a strong increase in abundance (more than 75%)
397 (Appendix S1: Figure S6). One hundred and fourteen species strongly decreased in frequency
398 from the 1980s to the 2020s (more than 75%) while 135 species strongly increased (more than
399 +75%) (Appendix S1: Figure S6).

400

401 **3. Shifts in weed community functional structure from the 1980s to the 2020s**

402 Community Weighted Means (CWM) of 13 traits were compared over the two periods
403 (Figure 4). Eight CWM out of 13 were significantly different over the two considered periods.
404 Weed communities from the 2020s had significantly lower leaf area (682 mm² on average in the
405 2020s and 937 mm² on average in the 1980s), higher SLA (23.3 m².kg⁻¹ on average in the 1980s
406 and 25.0 m².kg⁻¹ in the 2020s) and LDMC (181 mg.g⁻¹ in the 1980s and 198 mg.g⁻¹ in the 2020s)

407 (Figure 4). They were also characterised by a higher duration of flowering (4.3 months in the
408 1980s and 5 months in the 2020s) and earlier flowering species (May on average in the 1980s and
409 mid-April in the 2020s) compared to the 1980s communities. Moreover, the 2020s weed
410 communities were composed of species with lower seed mass (4.2 mg on average in the 1980s
411 and 3.5 mg in the 2020s), lower lateral spreadability, lower soil moisture requirement, and lower
412 proportion of C4 species (11% in the 1980s and 5% in the 2020s).

413 Over the two periods, weed communities of the Mediterranean vineyard network were
414 mostly ruderal (54% of R-score on average) and competitive (31% of C-score on average) while
415 they had 15% of stress-tolerance-score (Figure 5A). In the 2020s, at the global community pool
416 scale, weed communities were less competitive (27% of C-score) than in the 1980s (34% of C-
417 score) while they were more stress-tolerant (19% of S-score) than in the 1980s (12% of S-score)
418 (Figure 5A, B, C). The R-score was stable over the two periods (54% for both periods) (Figure
419 5D).

420

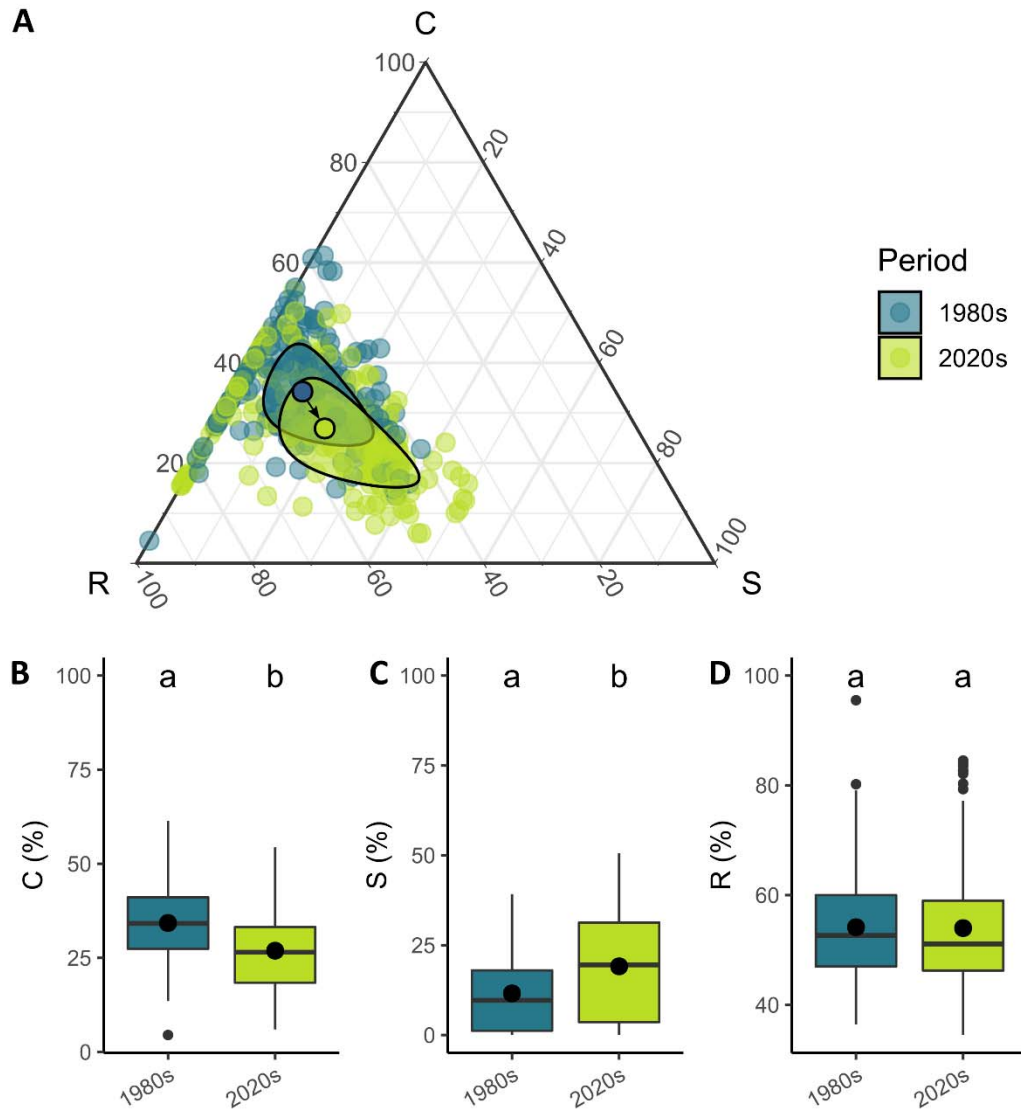


Figure 5A Shifts in CSR strategies of weed communities from the 1980s to the 2020s in Grime's triangle. Each dot is a community and their color indicates the period when the community was observed (blue, 1980s ; light green, 2020s). The two dots with black outlines are the barycentres of the communities of each period and the black ellipses represent the variance of the CSR strategies of the communities from the two periods. The arrow represents the shift in the mean strategy from the 1980s to the 2020s. Shifts in the proportion of competitive (B), stress-tolerance (C) and ruderal (D) strategies of weed communities from the 1980s to the 2020s. C, Competitors ; S, Stress tolerators ; R, Ruderal. n = 374 floristic surveys.

422 Using the elbow inflexion point method on the AUC, the first four dimensions of the CWM space
423 of the 1980s and the 2020s communities were selected (68.9% of total variance explained)
424 (Appendix S1: Figure S7). The first PCA axis opposed late and short-flowering communities to
425 early and long-flowering communities (Appendix S1: Figure S8A, Appendix S2: Table S2).
426 Weed communities of the 2020s were dominated by earlier and longer flowering species
427 compared to the 1980s communities (Appendix S1: Figure S8B, C). The second PCA axis was
428 mainly driven by soil moisture and species temperature requirement (Appendix S1: Figure S8A,
429 Appendix S2: Table S2). Weed communities from the 2020s were composed of species with
430 lower soil moisture requirements and were more thermophilic compared to the 1980s
431 communities (Appendix S1: Figure S8B, D). The third axis of the functional space was mainly
432 driven by the percentage of C4 species within the communities (Appendix S1: Figure S9A).
433 Current weed communities were composed of fewer C4 species compared to the 1980s
434 communities (Appendix S1: Figure S9B, C). Finally, the fourth axis was mostly driven by SLA
435 (Appendix S1: Figure S9A, Appendix S2: Table S2). This axis did not significantly discriminate
436 the 1980s from the 2020s weed communities (Appendix S1: Figure S9B, D). Many CWM
437 correlated significantly (Appendix S2: Table S3). Flowering onset was negatively correlated with
438 the duration of flowering ($\rho: -0.72, P < 0.001$) and positively correlated with maximum height
439 ($\rho: 0.75, P < 0.001$). The Ellenberg indices for temperature were positively related to Ellenberg
440 indice for light ($\rho: 0.64, P < 0.001$) (Appendix S2: Table S3).

441 **4. Drivers of the shift in weed community functional and taxonomic structures between** 442 **the 1980s and the 2020s**

443 Climate change, weed management trajectory from the 1980s to 2020s and the 2020s weed
444 management were not selected in the models explaining changes in abundance and diversity of

445 weed communities between the 1980s and the 2020s. Most of the variance was explained by the
446 vineyard identity and season random effects: 31% for the changes in abundance, 61% for the
447 changes in richness, 27% for the Shannon index and 9% for the Pielou index.

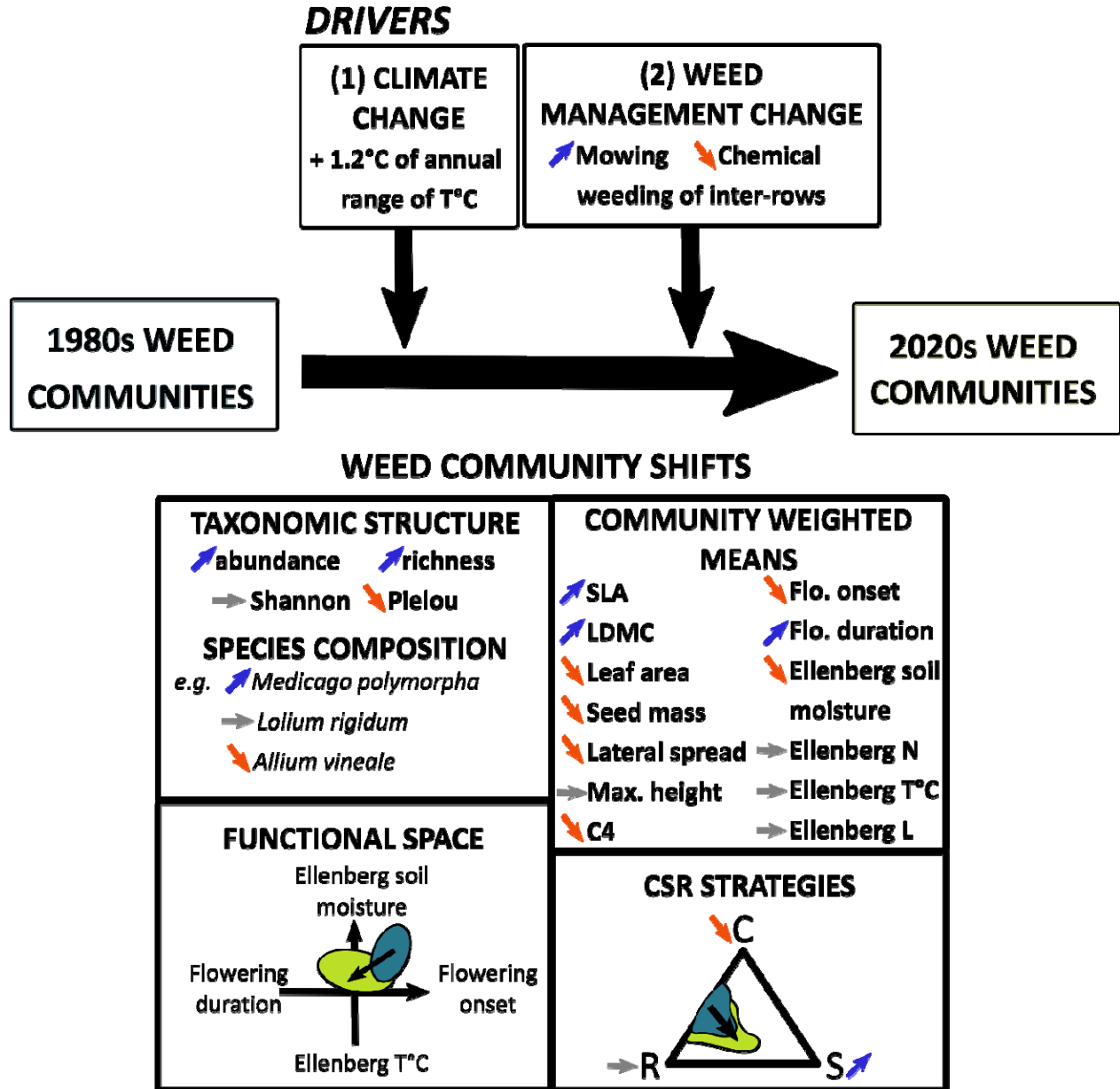
448 Climate change, the weed management trajectory from the 1980s to the 2020s and the
449 2020s weed management practices classified into four groups (Chem, Till, Till.IR.Chem.R,
450 Mow.IR.Till.R) were tested as explaining variables of the relative changes in functional
451 properties of weed communities between the 1980s and the 2020s. Vineyards that have
452 experienced a higher climate change intensity from the 1980s to the 2020s (*i.e.* vineyards located
453 in the northern part of the vineyard network, Figure 1) had more shifted to higher LDMC
454 weighted means than vineyards that experienced climate change to a lesser extent (*i.e.* vineyards
455 located nearby the Mediterranean Sea, Figure 1, Table 2). Weed communities that were
456 continuously sprayed with herbicides during the four decades had shifted toward lower CWM of
457 seed mass (-31% on average Appendix S1: Figure S10). Vineyards that were managed toward
458 more integrated weed management (*e.g.* vineyards managed entirely with tillage in the 1980s to
459 vineyard management with mowing, tillage and chemical weeding in the 2020s) were composed
460 of more C4 species in the 2020s than in the 1980s. For the other CWM, the fixed effects were not
461 selected in the final models, after model selection (Appendix S2: Table S4, S5, S6). Weed
462 communities that experienced a higher climate change intensity (*i.e.* higher relative change in
463 annual temperature range over the periods), had shifted toward more stress-tolerance strategies
464 and less ruderal strategies (Table 2). The shifts toward less competitive communities in the 2020s
465 were explained by the adoption of integrative weed management practices: vineyards that were
466 only managed by one type of weed management practice (tillage or chemical weeding) for four

467 decades had less shifted toward a lower score of competitive strategies compared to vineyards

468 where farmers adopted 1 or 2 other types of weed management practices.

469

470 DISCUSSION



471

472 Figure 6 Summary of the main findings of this study. Orange arrows represent significant

473 increases in the variables, blue arrows represent significant decreases and grey arrows represent

474 non-significant changes. Blue areas represent the functional properties of the 1980s communities

475 while green areas represent the functional properties of 2020s communities.

476 Four main findings were highlighted in this study. First, we demonstrated that climate change
477 occurred during the four decades of the study time scale through the increase of the annual range
478 of temperatures (Figure 6). Second, we found that weed management shifts from the 1980s to the
479 2020s were mostly characterised by the adoption of mowing and the ending of chemically
480 weeding of the inter-rows. Third, we described major shifts in weed community: (i) higher
481 abundance and richness and lower evenness, (ii) many species increased in abundance and
482 frequency (*e.g. Medicago polymorpha*) while fewer decreased (*e.g. Allium vineale*) and others
483 remained very stable (*e.g. Lolium rigidum*), (iii) community weighted means (CWM) of SLA and
484 LDMC increased, while CWM of leaf area, seed mass, lateral spread and the proportion of C4
485 decreased, (iv) weed communities shifted toward earlier and longer flowering, lower Ellenberg
486 indice of soil moisture and higher Ellenberg indice of temperature, (v) weed communities shifted
487 toward more stress tolerance strategies and less competitive strategies.

488 One of the main results of this study is that weed communities from the 2020s were 41%
489 more abundant and 24% more diverse in species than the 1980s communities at the vineyard
490 level. In arable lands, previous studies on weed changes over time showed drastic opposite
491 trends: -42% to -46% in species richness from the 1970s to 2000s (Fried, Dessaint, and Reboud
492 2016; Fried et al. 2009a) and -67% in species density (Fried et al. 2009b). The contrasts between
493 these studies and our results can be explained by a different temporal coverage. The period
494 1970s-2000s captured the strong filtering effect of herbicide adoption in arable lands before
495 changes in more extensive weed management practices in the 2000s (Fried et al., 2009a; Richner
496 et al., 2015). On the contrary, the two decades from the 2000s to the 2020s captured the effect of
497 the development of more extensive weed management. However, neither weed management
498 practice trajectory, nor climate change explained the shift in species abundance and richness.

499

500 **1. Significant changes in climate and weed management practices over four decades**

501 Climate shifted from the 1980s to the 2020s toward a higher annual range of temperatures (*i.e.*
502 the difference between the warmest month's and the coldest month's mean temperatures) that
503 averaged around 1.2 °C. Seasonal temperature fluctuations of climate are expected to occur under
504 climate change (Peters, Breitsameter, and Gerowitt 2014) and annual variability of temperatures
505 was the best predictor of climate change in our dataset. While the studies of climate change in the
506 Mediterranean area projected a decrease in precipitations (Ali et al. 2022), seasonal precipitation
507 variability over time explained fewer climate shifts than temperature metrics from the 1980s to
508 the 2020s. Precipitation variability within the vineyard network was greater than its variability
509 over time.

510 We hypothesised that weed management practices would evolve toward less chemical
511 weeding use and more frequent tillage and mowing from the 1980s to the 2020s (Cataldo, Fucile,
512 and Mattii 2021). Globally, weed management shifts matched our expectations and were driven
513 by the adoption of mowing of the inter-rows that replaced chemical weeding of the inter-rows.
514 More surprisingly, chemical weeding of rows and inter-rows was not widespread in 1978 and
515 1979 (*i.e.* the years of the first floristic surveys of this study) in the vineyard network. Indeed, 14
516 vineyards were managed using herbicides on both rows and inter-rows on 40 vineyards. Tillage
517 of rows and inter-rows was still quite commonly applied (9/40 vineyards). Chemical weeding
518 spread more widely in the decade that followed the end of the 1970s, a few years after the first
519 floristic surveys of this study. Maillet (1992) quantified for an extended network of vineyards
520 around Montpellier (that included the vineyard network of this study) that 41% of vineyards
521 shifted towards chemical weeding of both rows and inter-rows from 1979 to 1987. Moreover, in

522 the 1990s, the frequency of chemical weeding globally increased with a second application at the
523 end of spring to control for summer species (Maillet 1992). In our study, we did not consider the
524 shift in frequency of weed management and herbicide dose due to the difficulty of obtaining this
525 information from farmers for the decades between the 1980s and 2020s. Thus, if the median
526 management that was used in the 1980s and the 1990s is the same in our management trajectory
527 characterisation, it is most likely that 1990s weed management was more intensive in herbicide
528 use. We also did not explicitly consider in the characterisation of the weed management changes,
529 the active ingredients of herbicides that were different between the two periods. In the 1980s,
530 95% of herbicides used were simazine (pre-emergence) and aminotriazole-based (post-
531 emergence) (Maillet 1981). In the 2020s, herbicides were glyphosate-based (post-emergence
532 herbicide). If the spectrum of these herbicides from both periods was broad (*i.e.* targeting both
533 annuals and perennials), persistence over time was different: simazine can persist from three
534 months to 15 months while aminotriazole and glyphosate persist less than one month (Maillet
535 1981). Thus, in the 1980s, chemical weeding had a longer controlling action on weed
536 communities. This could explain for instance, that even the plots that were continuously
537 chemically weeded between the 1980s and the 2020s showed a slight increase of species richness
538 (13%).

539

540 **2. Climate change-induced weed community shifts toward more stress-tolerance**

541 According to our hypothesis, at the regional scale, weed communities shifted toward more stress
542 tolerance (+37% for S-score). Weed communities, that shifted toward a higher score of stress
543 tolerance from the 1980s to the 2020s, have also experienced a higher intensity of climate change
544 (*i.e.* a higher increase in annual temperature range). To our knowledge, this study is the first to

545 demonstrate that stress tolerance of weed communities is increasing in response to climate
546 change through changes in species composition.

547 The increase in stress tolerance is linked to the increase of the community-level leaf dry
548 matter content (181 mg.g⁻¹ in the 1980s and 198 mg.g⁻¹ in the 2020s) which is the *proxy* for stress
549 tolerance in Pierce et al.'s algorithm (2017). The increase in LDMC was also explained by the
550 increase in annual range temperatures in the selected models. This indicates that climate change
551 intensity reshuffled community composition toward more conservative species which invest in
552 leaves with thicker and stiffer cell walls that can maintain turgidity at low water potential
553 (Garnier et al. 2019). Other shifts of community-level traits indicated more conservative and
554 stress tolerance communities even though they were not significantly linked to the intensity of
555 climate change. For instance, leaf area decreased over time which has been related to a drought-
556 tolerance strategy (de la Riva et al. 2018). Ellenberg's indice of soil moisture of weed
557 communities also decreased significantly. Weed communities had earlier and longer flowering
558 times in the 2020s compared to the 1980s which could also be explained by a longer growing
559 season (Menzel et al. 2006). Surprisingly, the proportion of C4 species within the weed
560 communities decreased over time while it is expected that C4 species would increase with
561 climate change as their photosynthesis pathway is more efficient than those of C3 at higher
562 temperatures (Peters, Breitsameter, and Gerowitt 2014; Heilmeier 2019). However, independent
563 of temperature and precipitation changes, the increasing level of CO₂, which we did not consider,
564 has been predicted to favour C3 more than C4 (Peters, Breitsameter, and Gerowitt 2014). Indeed,
565 C3 weeds increase their leaf area and their biomass in higher CO₂ pressure than C4 species.
566 Thus, they are more competitive in such conditions.

567 **3. The diversification of weed management practices over time favoured less competitive**
568 **weed communities**

569 We hypothesised that the decrease in herbicide use replaced by tillage and mowing would favour
570 more conservative and competitive strategies for two reasons. First, mowing is a lower-intensity
571 disturbance than chemical weeding and would filter more conservative strategies than other
572 management practices (MacLaren, Bennett, and Dehnen-Schmutz 2019). Second, weed biomass
573 and competition for resources might be higher in mown communities, selecting competitive
574 species. In contrast with our expectations, communities from the 2020s were less competitive
575 than communities from the 1980s (34% of C-score in the 1980s versus 27% of C-scores in the
576 2020s) while mowing appeared in the 2000s in addition to the frequent tillage practice, resulting
577 in more complex weed management. A shift toward a higher diversity of weed management
578 practices and consequently more integrated management of weeds induced a higher decrease in
579 C-score. This strategy score is determined by leaf area in Pierce et al.'s algorithm (2017) which
580 also decreased over time. The diversity of disturbance types, intensity and frequency of integrated
581 managed vineyards favoured communities composed of species that did not invest in large leaf
582 areas and high maximum height (which was positively correlated to leaf area in our study) and
583 thus were less competitive to capture light. However, this was in contradiction with the higher
584 SLA of weed communities from the 2020s compared to the 1980s. Even though the effect of
585 integrated weed management on C-score was quite low (estimate: -0.20) and with a high *P*-value
586 (0.037), these results demonstrate that weed management is a lever of action to filter more
587 desirable weed communities that are less competitive with the main crops (MacLaren et al.
588 2020).

589 Weed communities continuously sprayed with chemical weeding for four decades shifted
590 toward lower seed mass (on average, -31% of seed mass at the community level) while those
591 where herbicides were interrupted for more than 20 years, showed the opposite trend (+22% of
592 seed mass). As seed mass is negatively correlated to seed number (Westoby 1998), weed
593 community strategies under chemical control are to produce a high number of seeds to face a
594 higher risk of seed mortality (Storkey, Moss, and Cussans 2010). Moreover, small seeds may
595 have higher seed dormancy (Thompson, Band, and Hodgson 1993) leading to a lower depletion
596 of the seed bank. In tilled vineyards, seeds can be buried in the top 5 centimetres of the soil after
597 tillage and are less exposed to desiccation. As heavier seeds are most likely to germinate when
598 they are buried (Benvenuti, Macchia, and Miele 2001), the weed community strategy under
599 tillage is to produce large seeds with a better probability of seedling establishment.

600 **4. Future weed communities: a threat or an opportunity for vineyards in the context of** 601 **climate change?**

602 The trend toward more stress-tolerant, less competitive and more diverse weed communities that
603 we identified for perennial cropping systems contrasted with several studies based on annual
604 cropping systems (Storkey, Moss, and Cussans 2010; Moss et al. 2004). In annual cropping
605 systems, the temporal increase in weed competitiveness was observed from 1969 to 2014 in the
606 Broadbalk Experiment, UK and was partly related to an increase in nitrogen input (Storkey et al.
607 2021). Fertilisation is a factor that we did not consider in our study management due to the
608 difficulty of obtaining this data from farmers. However, fertilisation amount in Mediterranean
609 vineyards is quite low (Metay et al. 2014) and the global temporal trend of fertilisation in
610 vineyards contrasted with the trend in annual cropping systems. Indeed, vineyard fertilisation has
611 decreased over the past decades with the aim of increasing wine quality (Verdenal et al. 2021)

612 and this trend could also explain the decrease in weed community competitiveness. Weed
613 management is a way for farmers to manage temporal variations in vine water supply which is a
614 key determining factor of crop productivity and fruit quality (Leeuwen et al. 2009). Changes in
615 weed management strategies (*e.g.* choice to sow a cover crop in the inter-rows) and weed
616 management tactics (*e.g.* choice of the date of weed destruction) are both needed to adapt to
617 higher temporal uncertainty, for short and long-term changes.

618 **Conclusion**

619 Using weed communities in Mediterranean vineyards as a model, we showed that
620 management and climate changes are modelling plant communities over time. The current shift
621 towards more extensive weed management in vineyards is driving more diverse and abundant
622 plant communities. In response to climate change, weed communities were more stress-tolerant.
623 The diversification of weed management techniques based on less herbicide use and more tillage
624 or mowing practices, at the plot level, drove less competitive weed communities. We showed that
625 the CSR framework is a relevant framework to assess changes in environmental conditions along
626 the resource gradient and shifts in management along the disturbance gradient. In this article, we
627 demonstrated that plant communities are adapting to climate change and that land management is
628 a strong lever for action to model diverse and functional plant communities.

629

630

631

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644

645 **Author contributions**

646 Marie-Claude Quido formatted the database. Marie-Charlotte Bopp led the writing of the
647 manuscript. All authors contributed critically to the drafts and gave final approval for publication.

648

649 **Conflict of Interest Statement**

650 The authors declare no conflict of interest.

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892 **Tables**

Table 1 Averaged climate and weed management characteristics in the 1980s and the 2020s. Minimum and maximum values are reported in brackets.

Drivers	Variables	Unit	1980s	2020s
Climate	Annual temperature range	°C	15.7 (15-16.9)	17.4 (16.2-18.1)
	Growing season length	Days	339 (328-353)	354 (337-363)
	Number of frost days	Days	11 (5-16)	23 (6-38)
	Winter rainfall	mm	312 (232-373)	144 (98-179)
	Spring rainfall	mm	228 (169-273)	207 (128-254)
	Summer rainfall	mm	125 (84-151)	104 (71-127)
	Autumn rainfall	mm	265 (166-337)	293 (187-362)
	Winter temperature	°C	7.1 (5.9-8.2)	7.4 (6-8.8)
	Spring temperature	°C	12.0 (10.8-12.9)	13.4 (12.2-14.5)
	Summer temperature	°C	21.0 (19.9-22.1)	23.1 (22.1-24.2)
	Autumn temperature	°C	13.8 (12.6-14.8)	15.2 (13.8-16.5)
	Management	Chemically weeded inter-rows	% of vineyards	35
Tilled inter-rows		% of vineyards	63	95
Mowed inter-rows		% of vineyards	0	78
Chemically weeded rows		% of vineyards	70	68
Tilled rows		% of vineyards	23	60

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Table 2 Standardised estimated coefficients of the explaining variables of the relative changes in community weighted means (CWM) and CSR strategies from the 1980s to the 2020s (C, Competitor ; S, Stress-tolerators ; R, Ruderal). Significant p -values ($P < 0.05$) are in bold. $n = 108$. *Std. est.* ; standardised estimates ; *Std. err.*, standardised errors ; t , t -value ; P , p -value.

	Explaining variables	<i>Std. est.</i>	<i>Std. err.</i>	t	P	Marginal R^2 / Conditional R^2
ΔCWM						
ΔSeed mass	#decades since herbicides were stopped	0.45	0.12	3.82	<0.001	0.20 / 0.52
ΔLDMC	Relative changes in the annual T°C range	0.46	0.11	4.26	<0.001	0.20 / 0.53
ΔC4	Shift toward integrated weed management	0.23	0.10	2.31	0.023	0.05 / 0.38
ΔCSR strategy						
ΔC	Shift toward integrated weed management	-0.20	0.10	-2.11	0.037	0.04 / 0.35
ΔS	Relative changes in the annual T°C range	0.46	0.10	4.71	<0.001	0.21 / 0.42
ΔR	Relative changes in the annual T°C range	-0.50	0.11	-4.33	<0.001	0.24 / 0.56

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