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ARTICLE

Climate and management changes over 40 years drove more stress-tolerant and less ruderal weed communities in vineyards

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Abstract

Spontaneous plant communities have undergone considerable constraints due to human-mediated changes. Understanding how plant communities are shifting in response to land management and climate changes is necessary to predict future ecosystem functioning and improve the resilience of managed ecosystems, such as agroecosystems. Using Mediterranean weed communities as models of managed plant communities in a climate change hotspot, we quantified the extent to which they have shifted from the 1980s to the 2020s in response to climate and management changes in vineyards. The weed communities of the same 40 vineyards in the Montpellier region were surveyed using the same protocol in spring, summer, and autumn, for two years, with a 40-year interval (1978–1979 vs. 2020–2021). In four decades, the annual range of temperatures (i.e., the difference between the warmest month's and the coldest month's mean temperatures) increased by 1.2°C and the summer temperatures by 2°C. Weed management diversified over time with the adoption of mowing that replaced the chemical weeding of interrows. Chemical weeding is now mostly limited to the area under the row. Current weed communities were 41% more abundant, 24% more diverse, and with a less even distribution of abundance across species than the 1980s communities at the vineyard level. Modern communities were composed of more annual species (57% of annual species in the 1980s vs. 80% in the 2020s) with lower community-weighted seed mass and were composed of fewer C4 species. They had higher community-weighted specific leaf area, higher leaf dry matter content, and lower leaf area than the 1980s weed communities. At the community level, the onset of flowering was earlier and the duration of flowering was longer in the 2020s. Climate change induced more stress-tolerant communities in the 2020s while the diversification of weed management practices favored less ruderal communities. This study shows that plant communities are shifting in

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response to climate change and that land management is a strong lever for action to model more diverse and eventually more desirable weed communities in the future.

KEYWORDS

40-year temporal changes, CSR strategies, global change, Mediterranean vineyards, trait-based approach, weed community, weed management change

INTRODUCTION

Spontaneous plant communities have undergone considerable constraints due to human-mediated changes (Inderjit et al., 2017). At the global scale, climate change results in higher temperatures, altered precipitation, higher frequency of extreme weather events, and increased levels of CO₂ (Peters et al., 2014). The Mediterranean area has been identified as a “climate change hotspot,” exceeding global warming average rates by 20% (Ali et al., 2022). The projections of the effect of climate change on plant communities are severe: decreased species richness, reduction in the species range, shifts toward a higher proportion of annual species in communities and a lower proportion of forbs (Pfeifer-Meister et al., 2016; Sala et al., 2000). These changes in plant composition can ultimately alter ecosystem processes (Cardinale et al., 2012). In the last 50 years, agriculture intensification including herbicides and mineral fertilizers uses has exerted strong selection pressures on spontaneous plant communities, promoting communities favored by a high level of disturbance and resources (Bourgeois et al., 2019). As a result of this more intensive weed management, the diversity of weed communities has also dramatically decreased in arable lands (Fried et al., 2016; Storkey et al., 2011, 2021).

In agroecosystems, the temporal changes in plant communities were mostly studied in annual cropping systems while few studies have investigated spontaneous flora shifts in less disturbed agroecosystems like perennial cropping systems. We assume that Mediterranean vineyard weed communities are particularly relevant models to study flora shifts because the agricultural practices of the vineyards strongly evolved from the late 1970s to the present. At the end of the 1970s, herbicides started to be widely applied on both the rows and the interrows of vines (i.e., the free space between the rows of vines) (Maillet, 1981). This constituted an abrupt change in environmental conditions resulting in drastic changes in weed communities (Maillet, 1992). In the 2000s, the awareness of the detrimental effects of herbicides on the environment (e.g., water quality) forced farmers to limit their use. Superficial tillage and mowing gradually replaced herbicide use in the interrows, leading to more

integrated weed management (Fernández-Mena et al., 2021). In addition, regulations are increasingly restricting the use of herbicides, with, for example, a ban on the use of glyphosate in the interrows of French vineyards from 2021 (ANSES, 2020). However, chemical weeding of the rows is still possible and frequent in French Mediterranean vineyards (Bopp, Fried, et al., 2022).

Trait-based approaches provide a relevant framework to better understand how weed communities shift in response to climate and management changes (Richner et al., 2015). Functional trait values at the community level respond to environmental filtering (e.g., climate change) (Lavorel & Garnier, 2002) and anthropogenic drivers (e.g., agricultural practices) (Booth & Swanton, 2002; Damour et al., 2018). This approach assumes that only certain species with specific trait values will persist within communities in particular climate and management conditions. Synchronic Mediterranean studies of trait patterns along aridity gradients (i.e., comparing simultaneously plant communities along the gradient) suggested that climate change promote communities with a more resource-conservative strategy: communities with small species, low leaf area and specific leaf area (SLA), and populations with short flowering duration (Costa-Saura et al., 2016; de la Riva et al., 2018; Nunes et al., 2017). Moreover, high temperatures and frequent drought would favor C4 weed species (Korres et al., 2016) and thermophilic species (Peters et al., 2014) while rising CO₂ atmospheric pressure is expected to favor C3 species. Thus, the impact of climate change on photosynthetic pathways is not entirely clear (Peters et al., 2014). Yet, few studies have revealed how climate change might modify plant communities using diachronic approaches (i.e., approaches that consider changes over time as opposed to synchronic approaches that explore changes using environmental gradient and simultaneous measurements) (Feeley et al., 2020; Harrison et al., 2020).

Weed management practices can be considered anthropogenic disturbances and can be classified according to their intensity and frequency (Gaba et al., 2014; Kazakou et al., 2016). For instance, chemical weeding and tillage represent both high-intensity

disturbances as they destroy the whole aboveground biomass (Kazakou et al., 2016). In contrast, mowing might be considered a lower intensity disturbance as this practice removes the aboveground biomass partially (MacLaren et al., 2019). Recent synchronic studies demonstrated the strong filtering effects of management on weed communities in vineyards (Kazakou et al., 2016; MacLaren et al., 2019). In this context, the CSR scheme of Grime (1977) can be a useful integrative approach to studying adaptive strategies that species use to cope with two constraints: (1) stress related to lower resource availability (e.g., water stress related to climate change in the Mediterranean area) and (2) disturbance related to the sudden destruction of biomass (e.g., weed management practices such as tillage, mowing, and chemical weeding). The CSR scheme describes three main species strategies: (1) stress tolerators (S) in resource-poor habitats with low disturbance, (2) ruderals (R) in resource-rich and highly disturbed environments (e.g., agroecosystems), and (3) competitors (C) in highly productive habitats with low-stress intensity and disturbance. If weed species are mostly ruderals as cultivated habitats are by definition regularly disturbed by tillage (Bourgeois et al., 2019; Mahaut et al., 2020), a recent study demonstrated that the proportion of CSR strategies in weed communities changed according to the weed management used (Fried et al., 2022). For instance, mowing favored communities with more competitive strategies (i.e., perennial species, with high seed mass, low SLA and high leaf dry matter content [LDMC]) while tillage favored species with more ruderal strategies (i.e., annual species with high SLA, low LDMC and late-flowering population) (Bopp, Kazakou, et al., 2022; Guerra et al., 2021; Hall et al., 2020; Mainardis et al., 2020). Climate change might also modify the relative proportion of species' CSR strategies within the communities over time (MacLaren et al., 2020). For instance, under climate change, weed species with stress tolerator strategies are more likely to occur (Korres et al., 2016). If recent synchronic studies exist in weed functional response to management (e.g., Hall et al., 2020; MacLaren et al., 2019) or to climate (Bopp, Kazakou, et al., 2022), no study, to our knowledge, has yet been conducted on weed community functional changes over time in vineyards.

In this study, we quantified how climate and management changes have shifted weed communities from the 1980s to the 2020s, using a historic group of vineyards of 40 Mediterranean vineyards in South France. First, we assessed climate change intensity and characterized changes in weed management practices in the study group of vineyards. Then, we described shifts in taxonomic, phylogenetic, and functional weed community structures after four decades using 374 floristic surveys that were performed during two years at each period (1978, 1979, 2020, 2021) and at three seasons (spring

[March], summer [June], autumn [October]). Finally, we tested whether climate conditions and weed management practices drove changes in weed community structure between the 1980s and the 2020s. We hypothesized that climate change would favor species with more water-conservative traits (e.g., C4 metabolism, small leaf area, high LDMC) and stress-tolerant strategies. Moreover, we expected that the decrease in herbicide use replaced by mowing would favor more conservative and less ruderal strategies.

MATERIALS AND METHODS

Climate, soil, and weed management characterization of the historical group of vineyards

The historical group of vineyards was composed of 40 vineyards located around Montpellier, France (Figure 1). These study sites were first set up in 1978 to study weed management effects on weed community composition (Maillet, 1981). The vineyards are located in a Mediterranean climate characterized by warm temperatures: 14°C mean annual temperatures on average from 1978 to 2021, 814 mm per year of rainfall, and dry summers (88% of annual precipitation occurs during the other seasons). Soil textures of vineyards varied along a northeast/southwest gradient determined by the distance to the Mediterranean Sea: from sandy vineyards near the sea to loamy and clay/loamy soils in further northeast vineyards.

To characterize climate change per decade from the 1980s to the 2020s, variables describing seasonal and annual climate were extracted from the estimations obtained by the SAFRAN interpolation method (analysis system providing atmospheric information to the snow) on an 8 × 8 km² grid (Durand et al., 1993) from 1971 to 2021. Eleven variables were selected: mean seasonal temperatures and total rainfall per season (spring, summer, autumn, and winter), growing season length (GSL) (i.e., the number of days in a year with daily mean temperature above 5°C during at least six consecutive days), number of frost days and annual range of temperatures (i.e., the difference between the warmest month's and the coldest month's mean temperatures). To characterize the climate change trajectory between the 1980s and 2020s, all these variables were averaged over five different decades from 1971 to 2021 (1971–1980; 1981–1990; 1991–2000; 2001–2010; 2011–2021). Due to the SAFRAN grid, 31 neighboring vineyards on 40 shared the same climate data at least with another vineyard: 20 squares of 8 × 8 km² with different climate data were used for the 40 vineyards.

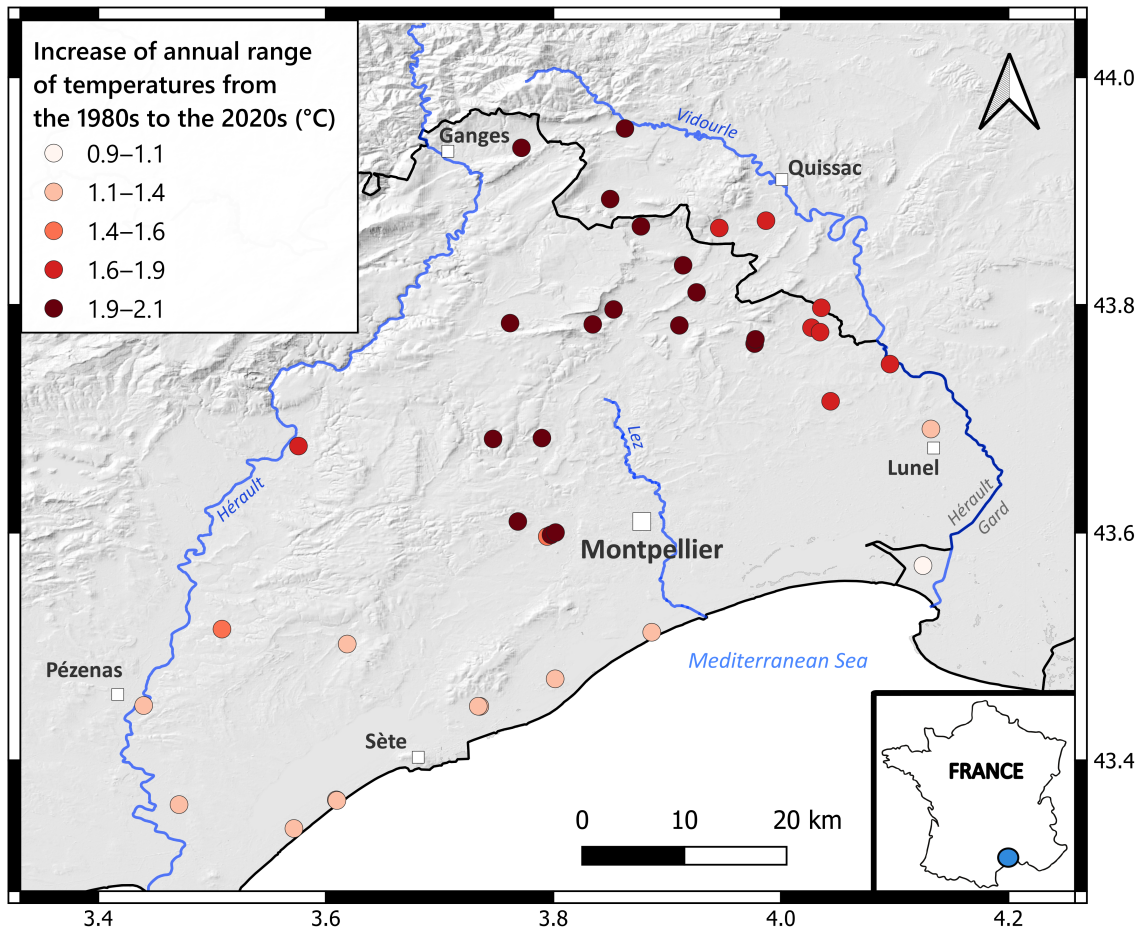


FIGURE 1 Geographical distribution of the increase in the annual range of temperatures from the 1980s to the 2020s experienced by the 40 vineyards of the study sites, Montpellier, France. Each dot is a vineyard and its color represents the extent of the increase in the annual range of temperatures (from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

To characterize changes in weed management practices of the rows and the interrows from 1978 to 2021, we conducted interviews with each farmer of the network (see Appendix S1: Section S1). To characterize weed management in the 1980s (“initial state”) and in the 2020s (“final state”), we computed the annual frequency of mowing, tillage, and chemical weeding of the rows and the interrows (Table 1). Some farmers applied one practice (e.g., mowing) on half of their interrows and another practice on the other half (e.g., tillage). In that case, we considered that the annual frequency of mowing and tillage was divided by 2. To characterize weed management shift, we considered the three following variables: (1) the number of years since mowing was adopted by the farmers in the vineyards, (2) the number of years since herbicides were abandoned, and (3) weed management diversification: the number of additional weed management practices applied in the 2020s compared with the 1980s (Table 1). For instance, if a vineyard was only managed with tillage in the 1980s but managed with both tillage

and mowing in the 2020s (i.e., mowing was the additional practice), the value of the management diversification variable would be “1.”

Weed community composition in the 1980s and the 2020s

Weed community composition was determined in 1978 and 1979 (as “1980s communities” hereafter) (Maillet, 1981) and in 2020 and 2021 (as “2020s communities”) at three different seasons (late winter [March], early summer [June], and autumn [October]) (Appendix S2: Figure S1). In total, the dataset was composed of 374 floristic surveys (for more details, see Appendix S2: Figure S1). To compare the floristic compositions over the two periods, we applied the same method of floristic surveys. In each vineyard, a rectangular area of 400 m² (40 × 10 m²) was delimited (four interrows and three rows of the same length). To estimate species abundance, we used five abundance classes

TABLE 1 Mean and SD of fixed effects of the linear mixed models to explain taxonomic, phylogenetic, and functional shifts in weed communities from the 1980s to the 2020s.

Type of explaining variable	Explaining variable	Description (values)	Mean ± SD
Timing of floristic surveys	Season	Season of floristic survey (Mar, Jun, Oct)	
Climate change	ΔT.Summer	Shift in annual summer temperature	0.05 ± 0.002
	ΔT.Range	Shift in annual temperature range (i.e., the temperature difference between the hottest and coldest months)	0.046 ± 0.01
1980s management	Nb.Chem.IR.1980	Annual frequency of herbicide sprayings of the interrow in the 1980s	0.2 ± 0.4
	Nb.Chem.R.1980	Annual frequency of herbicide sprayings of the rows in the 1980s	0.6 ± 0.5
2020s management	Nb.Chem.IR.2020	Annual frequency of herbicide sprayings of the interrow in the 2020s	0.2 ± 0.30
	Nb.Chem.R.2020	Annual frequency of herbicide sprayings of the rows in the 2020s	1.0 ± 0.8
	Nb.Till.IR.2020	Annual frequency of tillage of the interrow in the 2020s	2.3 ± 0.3
	Nb.Mow.IR.2020	Annual frequency of mowing of the interrow in the 2020s	0.8 ± 0.7
1980s to 2020s trajectory	Nb.decades.stop.Chem	No. decades since herbicides were abandoned	0.6 ± 1.0
	Nb.decades.start.Mow	No. decades since mowing was adopted	1.7 ± 0.9
	Practices_diversification	Weed management diversification: no. additional weed management practices applied in the 2020s compared to the 1980s	1.2 ± 0.6

developed by Barralis (1976): “1,” less than 1 individual/m²; “2,” 1–2 individuals/m²; “3,” 3–20 individuals/m²; “4,” 21–50 individuals/m²; “5,” more than 50 individuals/m². We transformed these scores into a quantitative scaling using the median of the range of each density class as follows: “1,” 0.5 individual/m²; “2,” 1.5 individuals/m²; “3,” 11.5 individuals/m²; “4,” 35.5 individuals/m²; “5,” 75 individuals/m². A list of species and distinct abundance scores were noted at the plot level. To control the “observer effect,” we conducted several floristic surveys in 2020 with Jacques Maillet, who conducted the floristic surveys in the 1980s. No major biases were observed during these floristic surveys. For each community, we computed the richness, the abundance (i.e., the sum of the density of each species), the Shannon diversity index, and Pielou’s evenness index (Pielou, 1966). Based on existing vascular plant phylogeny (mega tree “GBOTB.extended.TPL.tree”), we computed phylogenetic distance-based Rao’s quadratic entropy (i.e., pairwise distances between the pairs of tips from the phylogenetic tree using its branch lengths) for the 1980s and the 2020s communities, following Tucker et al. (2017), using “V.PhyloMaker2” package (Jin & Qian, 2022).

Functional properties of the 1980s and 2020s weed communities

Seven plant traits, two phenological population-level traits, and four Ellenberg indices were selected to analyze

plant responses to climate change and weed management changes. Three traits of the Leaf-Height-Seed (LHS) strategy scheme were selected (Westoby, 1998): (1) SLA (in square meters per kilogram) related to the speed of resources acquisition (Wright et al., 2004), (2) maximum height (in meters) related to light and nutrient acquisition (Westoby et al., 2002), (3) seed mass (in grams) which represents the “colonization-competition” trade-off (Moles & Westoby, 2006). Leaf area (in square meters) was also selected as a good proxy for the competitive abilities of plants. LDMC (i.e., the ratio between leaf dry mass and leaf fresh mass) was selected as a proxy for plant investment in leaf. Photosynthesis pathways (C3/C4) were assessed to identify the species with water-saving photosynthesis (Pyankov et al., 2010). Phenology was characterized by the months of flowering onset (i.e., when half of the individuals of a species have bloomed) and the number of months of flowering determined at the population level for each species. Species resource requirements were characterized through four Ellenberg indices: light (EIV_L), temperature (EIV_T), soil moisture (EIV_F), and nitrogen (EIV_N). Raunkiaer plant life forms were included.

Leaf area, SLA, and LDMC were measured on the weed species present in the 2020s communities (8 individuals per species). The other traits were extracted from different databases: Seed Information Database for seed mass (Royal Botanic Gardens Kew, 2021), *Flora Gallica* for maximum height (Tison & De Foucault, 2014), Baseflor for flowering onset, duration of flowering, and

the four Ellenberg indices (Julve, 1998). Flowering onset and duration of flowering are quantified at the population level and not at the individual level (i.e., a long flowering duration does not mean that individuals of that species can flower during a long period but that different individuals of that species cover together a long period of flowering). Photosynthetic pathways were extracted from Pyankov et al. (2010).

To scale up the trait values from the species level to the community level, we calculated the community weighted means (CWM) of the traits (i.e., the average of the trait values of species present in a community, weighted by their relative abundances) (Garnier et al., 2004) using at least 80% of the most abundant species of the weed communities in the calculation (mass ratio hypothesis, Grime, 1998). This means that for each community, species were arranged in descending order of abundance, and the CWM were calculated based on species whose combined abundances constitute at least 80% of the total abundance (starting with the most abundant species and summing the abundances of others in descending order). We calculated median values for the percentage of C4 species' abundance within the communities. Based on the CWM of SLA, LDMC, and leaf area, we calculated the competitiveness (C), stress-tolerance (S), and ruderal (R) scores following Pierce et al. (2017) and Li and Shipley (2017). Based on the CWM, we computed a trait distance-based Rao's quadratic entropy to characterize functional diversity.

Data analyses

Description of climate, weed management, and weed community functional structure using multivariate analyses

Multivariate analyses were performed to characterize climate change per decade from the 1980s to the 2020s (1980s, 1990s, 2000s, 2010s, and 2020s) (see Appendix S1: Section S2). Before performing the principal components analysis (PCA) based on climate variables, we removed the variables that were too highly correlated (Pearson correlations >0.8). Four variables were then selected: the mean summer temperature, the summer rainfall, the annual range of temperature, and the GSL (i.e., the number of days in a year with daily mean temperature above 5°C during at least six consecutive days). A PCA was also performed on the CWM of the traits of the 1980s and 2020s communities. To select a parsimonious number of dimensions to represent well the functional space, we used the elbow inflection point method on the area under the curve (AUC) and the mean absolute deviation (MAD) following Mouillot et al. (2021).

Comparison of structure and composition of the 1980s and 2020s weed communities

Two different datasets were used for data analyses (Appendix S2: Figure S1). The first one is the “full dataset” composed of the 374 floristic surveys from the 1980s and the 2020s. This dataset was used to test the significance of the difference in means of taxonomic indices (abundance, richness, Shannon, Pielou), phylogenetic and functional diversity indices, Raunkiaer plant life forms, and CWM and CSR scores over time. Using the full dataset ($n = 374$), we fitted linear mixed models with the period (the 1980s/2020s) as a fixed effect and the season (March/June/October), the year (1978, 1979, 2020, 2021), and plot identity as random effects. Before constructing the models, we checked the collinearity and the variation inflation factors (vif) of the explaining variables. An ANOVA was performed on these models to test fixed effect significance. Post hoc Tukey and Wilcoxon tests were then computed to assess the direction of the changes in properties of weed communities from the 1980s to the 2020s. Moreover, the changes in abundance and frequency of species over time were quantified using indices of relative changes following the formula:

$$\Delta\text{Index} = \frac{\text{Index}_{2020s} - \text{Index}_{1980s}}{\text{Index}_{2020s} + \text{Index}_{1980s}} \quad (1)$$

These indices varied from -1 to 1 . From these indices, we identified (1) the species that increased in abundance and frequency defined as the species with more than 0.75 of relative changes in abundance and frequency, (2) the species that decreased in abundance and frequency with less than -0.75 of relative changes, and (3) the species that remained stable in abundance and frequency with relative changes within the range of $[-0.75; 0.75]$.

Identification of the drivers of weed community structure shifts over time

The second dataset was built to test whether climate and management changes explained the changes in taxonomic, phylogenetic, and functional properties of weed communities (Appendix S2: Figure S1). To build an “explaining” dataset, we averaged the functional, phylogenetic, and taxonomic metrics over the two years for each period (1978 and 1979 for the 1980s communities, and 2020 and 2021 for the 2020s communities): from five floristic surveys per period (e.g., for the 1980s, March 1978, 1979, June 1978, 1979, and October 1979) to three floristic surveys per period (e.g., March 1980s, June 1980s, October 1980s). Then, each season of each period

was comparable with the season of the other period (e.g., March 1980s with March 2020s). This “explaining” dataset was composed of 120 taxonomic, phylogenetic, and functional shifts of communities from the 1980s to the 2020s: 40 vineyard community shifts \times 3 seasons (Appendix S2: Figure S1). After removing missing data about management practices for four vineyards and their three associated seasons (i.e., 12 shifts missing), the dataset consisted of 108 shifts. We used two different ways of computing indexes of shifts: (1) For comparing coordinates of the CWM in the functional PCA, we computed the difference between the coordinates in the 2020s and the coordinates in the 1980s for each selected axes of the multivariate analysis and (2) for comparing “raw values” of different metrics (CWM, CSR scores, annual temperature range, abundance, richness, Shannon and Pielou indices, functional and phylogenetic diversity), we computed indices of relative changes using Equation (1). As a *proxy* for climate change, we selected the relative changes in the annual temperature range between the 1980s and the 2020s (i.e., the difference between the warmest month’s and the coldest month’s mean temperatures) and the mean summer temperature that explained most climate change from the 1980s to the 2020s. To describe past and current weed management, we used six variables describing the annual frequency of application of each existing management method on the row (R) and interrow (IR) for each period: (1) the number of herbicide treatments in the 1980s on the row (Nb.Chem.R.1980) and (2) on the interrow (Nb.Chem.R.1980), (3) the number of herbicide treatments in the 2020s on the row (Nb.Chem.R.2020) and (4) on the interrow (Nb.Chem.IR.2020), (5) the number of tillage operations on the interrow in 2020s (Nb.Till.IR.2020), (6) the number of mowing operations on the interrow in 2020 (Nb.Mow.IR.2020) (Table 1). Cover crops (with barley, *Hordeum vulgare*) were only used on the same four plots, in the 1980s and 2020s. Therefore, we did not consider this variable in explaining the changes. Irrigation is a practice that appeared on 10 plots, where it is done through drip irrigation (preliminary analysis showed no effect of this practice, likely because only the row is irrigated, representing a small area compared to the entire sampled vegetation). Thus, we did not consider this variable.

Using the “explaining” dataset ($n = 108$), we fitted linear mixed models to explain the shifts in CWM, taxonomic indices (abundance, richness, Pielou, Shannon), phylogenetic and functional diversity indices, and CSR scores over time. We included the following explaining variables as fixed effects in the models (Table 1): (1) the season of the floristic survey (March, June, October), (2) the shift in annual summer temperature and annual

range of temperatures (i.e., the temperature difference between the hottest and coldest month) as *proxies* of climate change, computed using Equation (1), (3) the annual frequency of chemical weeding, tillage and mowing of rows and interrows in the 1980s and in the 2020s as “initial” and “final” management descriptors, (4) the number of years since herbicides were abandoned, (5) the number of years since mowing was adopted, and (6) weed management diversification (i.e., the number of additional weed management practices applied in the 2020s compared with the 1980s). We added a plot identity effect as a random effect. Before performing the mixed models, we removed the explaining variables with high *vif* ($> :5$): (1) the annual frequency of row tillage in the 2020s was removed as it was too anticorrelated with the annual frequency of row chemical weeding in 2020s ($\rho = -0.74$, $p < 0.05$), (2) the annual frequency of row and interrow tillage in the 1980s were removed as they were too anticorrelated with chemical weeding of rows ($\rho = -0.91$, $p < 0.05$) and interrows ($\rho = -0.76$, $p < 0.05$), respectively. The selection of models was done based on the corrected Akaike information criterion (AIC_c) with the dredge function from the MuMIn R package (Burnham & Anderson, 2002). The first best models were selected with $\Delta AIC < 2$ condition. All data analyses were carried out using R version 4.1.1 (R Core Team, 2021).

RESULTS

Climate and management changes from the 1980s to the 2020s

Climate change from the 1980s to the 2020s

Over the two periods, the climate variables (mean summer temperature, summer rainfall, GSL, and annual ranges of temperatures) were well explained by the first two PCA axes (85.8% of total variance) (Figure 2). The first axis was driven by the summer rainfall (38% of the contribution), the mean summer temperatures (34% of the contribution), and GSL (27% of the contribution). This axis opposed vineyards located in areas with warm and dry climates with longer GSL (i.e., vineyards near the coastline, Figure 1) to vineyards located in areas with high rainfall, colder temperatures, and lower GSL (i.e., vineyards located in the northeast of the study sites, Figures 1 and 2). The second axis was driven by the annual range of temperatures (64% of contribution). In 40 years, the summer mean temperatures have increased by $2^\circ\text{C} \pm 0.26$ (21°C in the 1980s and 23°C in the 2020s, Table 2). The annual range of

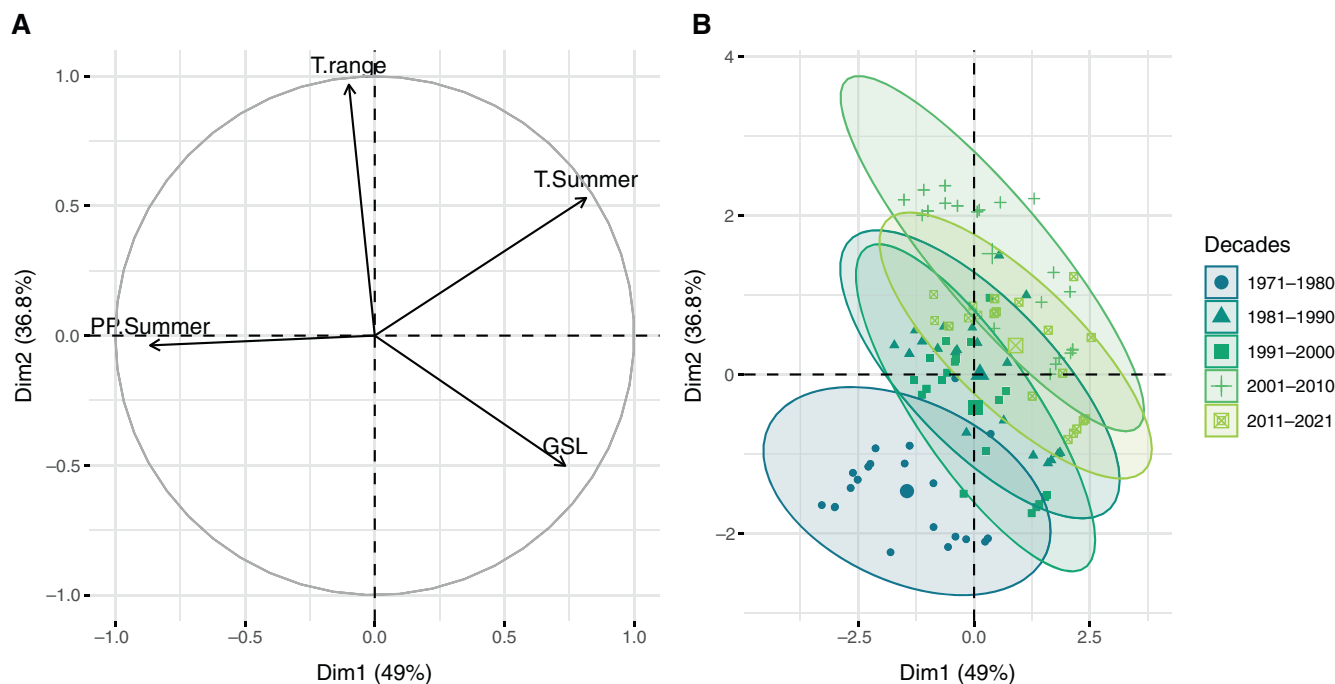


FIGURE 2 Climate change from the 1970s to the 2020s. (A) Correlation circle of the climate variables on the first two axes of the climate principal components analysis (PCA) over the decades from the 1970s to the 2020s. (B) Vineyard projection on the first two axes of the climate PCA for each decade 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. Each dot is the climate of one of the 40 vineyards and its color refers to the decade. GSL, growing season length; PP.Summer, summer cumulated rainfall (in millimeters); T.range, annual temperature range (in degrees Celsius); T.Summer, mean summer temperature (in degrees Celsius).

TABLE 2 Averaged climate and weed management characteristics in the 1980s and the 2020s.

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)
	Summer rainfall	mm	125 (84–151)	104 (71–127)
	Summer temperature	°C	21.0 (19.9–22.1)	23.1 (22.1–24.2)
Management	Chemically weeded interrows	% of vineyards	35	28
	Tilled interrows	% of vineyards	63	95
	Mowed interrows	% of vineyards	0	78
	Chemically weeded rows	% of vineyards	70	68
	Tilled rows	% of vineyards	23	60

Note: Minimum and maximum values are reported in brackets.

temperature increased by $1.2^{\circ}\text{C} \pm 0.4$ (15.7°C in the 1980s and 17.4°C in the 2020s, Table 2). Based on these PCA results, we selected the mean summer temperature and the annual range of temperatures as *proxies* of climate change because they had the highest coefficients of correlation with the first two axes (ρ : 0.87, $p < 0.001$ for the mean summer temperature and the first dimension; ρ : 0.95, $p < 0.001$ for the annual range of temperatures and the second dimension).

Weed management shifts from the 1980s to the 2020s

From the 1980s to the 2020s, weed management changes were mainly characterized by the adoption of mowing (Table 2). In the 1980s, mowing did not exist while vineyard interrows were mowed on average 0.8 ± 0.7 times per year in the 2020s. In the 2020s, 53% of vineyards were managed with one mowing per year, 28% of vineyards

with two mowings per year and only 19% were not managed using mowing (Figure 3E). The frequency of tillage and chemical weeding was quite similar in the 1980s and in the 2020s. On average, interrows were tilled 2.3 ± 1.7 times per year in the 1980s and 2.3 ± 1.4 in the 2020s. In the 1980s, most of the farmers applied 4 tillage or more in the interrows (for 44% of the vineyards, Figure 3C) while it was mainly 2 tillage in the 2020s (for 33% of the vineyards, Figure 3C). Rows were tilled 0.8 ± 0.5 times per year in the 1980s and 0.6 ± 0.8 times per year in the 2020s. The interrows were managed with 0.3 ± 0.5 herbicide sprayings per year in the 1980s and with 0.2 ± 0.3 sprayings in the 2020s: 19% of vineyards were sprayed at least once a year in the 1980s while 5% of the vineyards were sprayed at least once a year in the 2020s (Figure 3A). Most of the vineyards were managed with less than one spraying in the 2020s (25% of vineyards, Figure 3A). The rows were managed with 0.6 ± 0.5 sprayings in the 1980s and 1 ± 0.8 sprayings in the 2020s. In the 1980s, most of the rows were managed with one spraying (53% of vineyards) while 28% of vineyards were managed with two sprayings in the 2020s and 25% with one spraying (Figure 3B). In the 2020s, some farmers applied different practices in different interrows: for instance, mowing on half of the interrows and tillage on the other half was applied in 11 vineyards.

From the 1980s to the 2020s, 61% of vineyards were managed with an additional practice (mainly mowing), 28% were managed with two additional practices (mostly mowing and chemical weeding), and 11% were managed with the same number of different practices (Figure 3F). Most of the vineyards were managed with continuous spraying of herbicides (70%) while 22% of farmers abandoned herbicides in the 2000s and 6% in the 2010s (Figure 3G). Twenty-two per cent of the farmers adopted mowing in the 1990s, 33% in the 2000s (33%), and 39% in the 2010s (Figure 3H).

Shifts in weed community structure from the 1980s to the 2020s

In total, 436 species were found over the 374 floristic surveys of the two periods. At the vineyard group scale, a similar number of species were identified 40 years apart: 320 species in the 1980s and 319 species in the 2020s. At the vineyard scale, the mean species richness was higher in the 2020s (34 ± 13 species/community) than in the 1980s (26 ± 13 species/community) (Figure 4). Community density showed the same trend as species richness: 68 ± 45 individual plants/m² were found in the 2020s while 40 ± 36 individual plants/m² were found in the 1980s. However, Shannon diversity was not significantly different between the two periods (2.39 ± 0.60 in

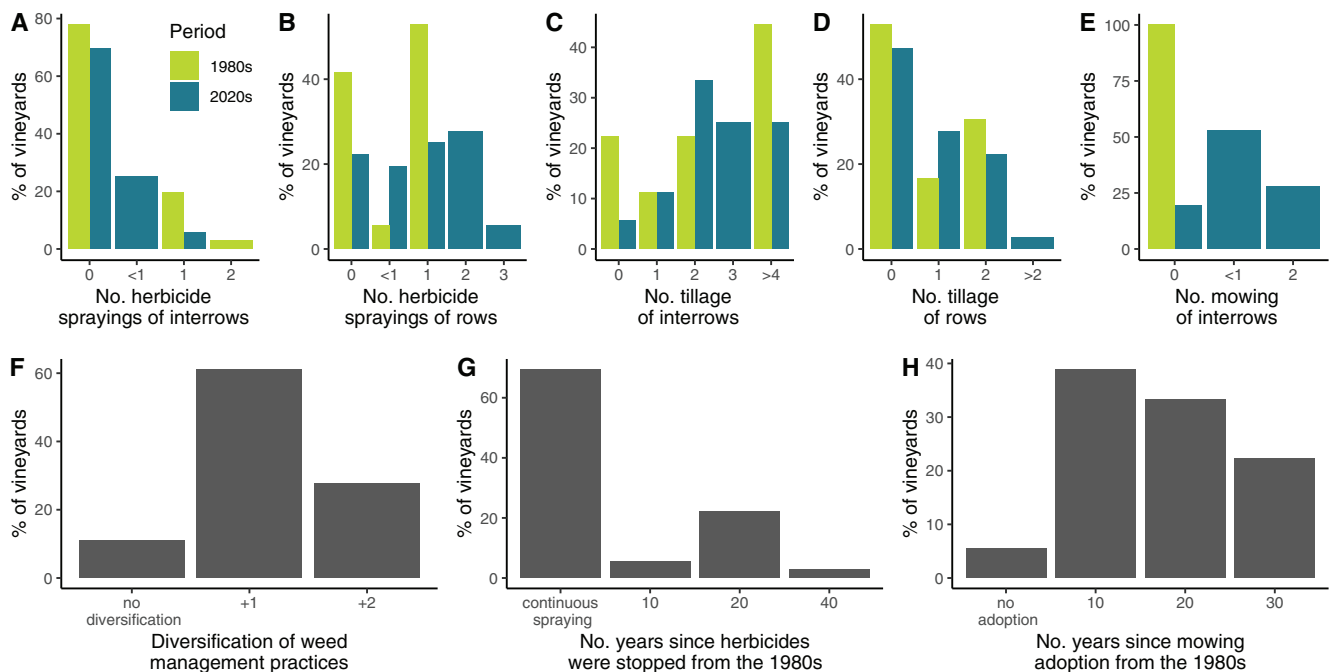


FIGURE 3 Weed management changes from the 1980s to the 2020s. The annual number of herbicide sprayings of interrows (A) and rows (B), in the number of tillage of interrows (C) and rows (D), and in the number of mowing of interrows (E) applied in the vineyards in the 1980s compared to the 2020s. Proportion of vineyards with diversification of weed management practices (F). Timing of herbicide abandonment (G) and mowing adoption (H).

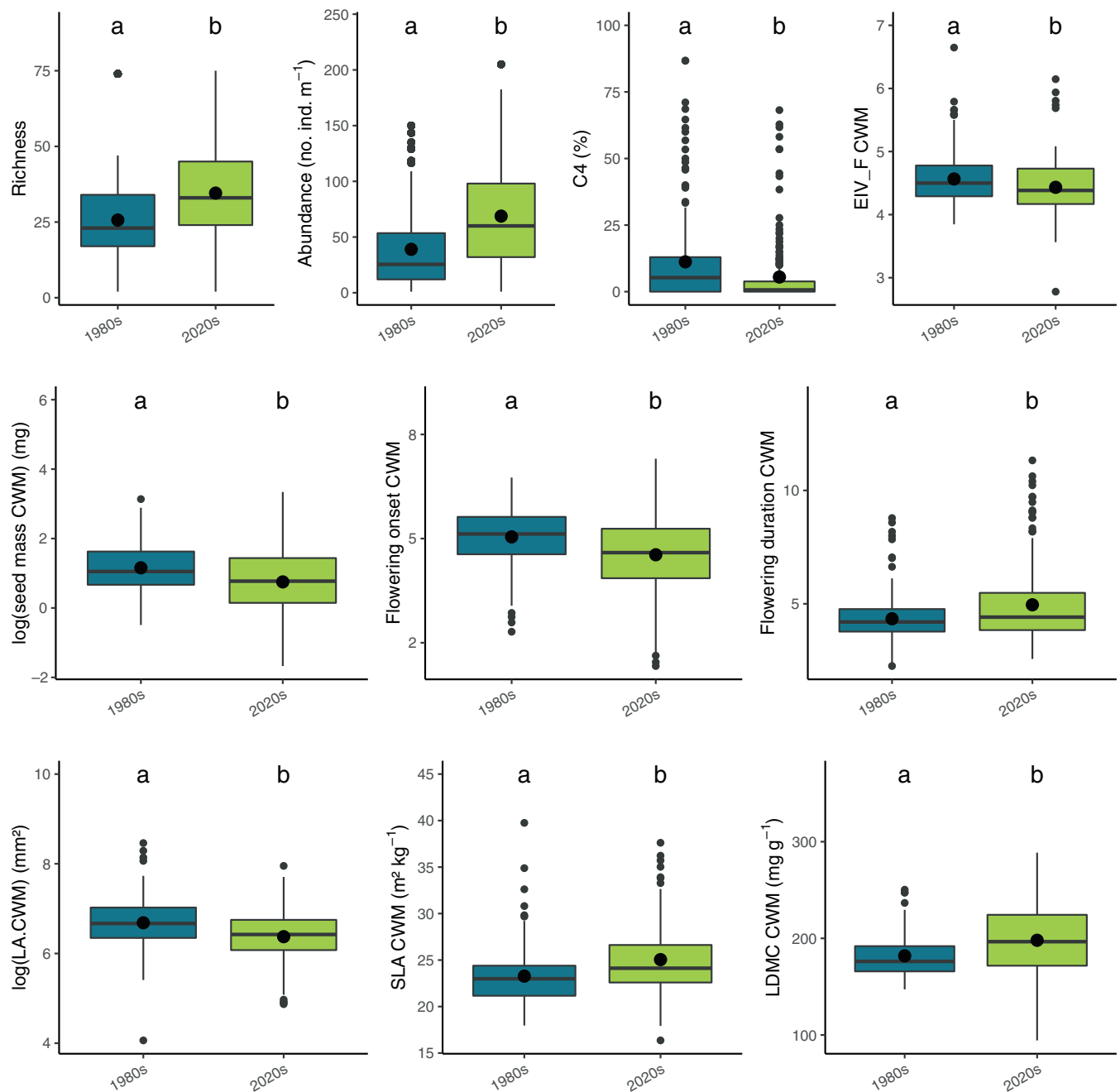


FIGURE 4 Significant changes in abundance, richness, and functional properties of weed communities between the 1980s and the 2020s. Different letters indicate significant differences based on post hoc Tukey and Wilcoxon tests. Note that the scale of the y-axis varies between the sub-figures. CWM, community weighted means; EIV_F.CWM, Ellenberg indice for soil moisture; LA, leaf area; LDMC, leaf dry matter content; SLA, specific leaf area. $n = 374$ floristic surveys.

the 2020s and 2.40 ± 0.59 in the 1980s) and the Pielou index was significantly lower in the 2020s (0.69 ± 0.17 in the 2020s and 0.78 ± 0.18 in the 1980s). This showed that the 2020s community were less equitable in abundance (Appendix S2: Figure S2). Phylogenetic diversity was similar in the 1980s (phylogenetic Rao's indice: 0.78 ± 0.17) and in the 2020s (phylogenetic Rao's indice: 0.77 ± 0.14).

The 2020s weed communities were composed of more therophytes compared with the 1980s communities

(57% of the species in the 1980s compared with 80% in the 2020s) (Appendix S2: Figure S3). In contrast, the 1980s communities were composed of more bulb geophytes (e.g., *Allium vineale*): 7% of bulb geophytes composed the 1980s communities while they represented 1% of the weed communities in the 2020s. The 1980s weed communities were composed of more rhizome geophytes (e.g., *Cynodon dactylon*) (10% in the 1980s vs. 4% in the 2020s), more biennial hemicryptophytes (e.g., *Chondrilla*

juncea) (7% in the 1980s vs. 5% in the 2020s), more cespitose and erected hemicryptophytes (e.g., *Anthemis maritima*) (8% in the 1980s and 6% in the 2020s), and more hemicryptophytes with stolons (e.g., *Convolvulus arvensis*) (9% in the 1980s vs. 3% in the 2020s).

Out of 423 species, 73 species had a strong decrease in abundance from the 1980s to the 2020s (more than 75% decrease) while 116 species had a strong increase in abundance (more than 75%) (Appendix S2: Figure S4). One hundred fourteen species strongly decreased in frequency from the 1980s to the 2020s (more than 75%) while 135 species strongly increased (more than 75%) (Appendix S2: Figure S4).

Shifts in weed community functional structure from the 1980s to the 2020s

CWM of the traits were compared over the two periods (Figure 4). Eight of 12 CWM were significantly different over the two considered periods. Weed communities from the 2020s had significantly lower leaf area ($682 \pm 407 \text{ mm}^2$ on average in the 2020s and $937 \pm 588 \text{ mm}^2$ on average in the 1980s), higher SLA ($23.3 \pm 3.0 \text{ m}^2 \text{ kg}^{-1}$ on average in the 1980s and $25.0 \pm 3.7 \text{ m}^2 \text{ kg}^{-1}$ in the 2020s), and LDMC ($181 \pm 21 \text{ mg g}^{-1}$ in the 1980s and $198 \pm 37 \text{ mg g}^{-1}$ in the 2020s) (Figure 4). They were also characterized by a higher duration of flowering (4.3 ± 1.1 months in the 1980s and 5 ± 1.7 months in the 2020s) and earlier flowering species (May on average in the 1980s and mid-April in the 2020s) compared with the 1980s communities. Moreover, the 2020s weed communities were composed of species with lower seed mass ($4.2 \pm 3.5 \text{ mg}$ on average in the 1980s and $3.5 \pm 5.1 \text{ mg}$ in the 2020s), lower soil moisture requirement (4.57 ± 0.38 in the 1980s and 4.43 ± 0.44 in the 2020s), and lower proportion of C4 species ($11\% \pm 17$ in the 1980s and $5\% \pm 12$ in the 2020s). Functional diversity was similar in the 1980s (0.014 ± 0.002) and in the 2020s (0.014 ± 0.002).

Over the two periods, weed communities of the Mediterranean vineyard group were mostly ruderal ($54\% \pm 11$ of R-score on average) and competitive ($31\% \pm 11$ of C-score on average) while they had $15\% \pm 14$ of stress-tolerance score (Figure 5A). In the 2020s, at the global community pool scale, weed communities were less competitive ($27\% \pm 10$ of C-score) than in the 1980s ($34\% \pm 10$ of C-score) while they were more stress-tolerant ($19\% \pm 15$ of S-score) than in the 1980s ($12\% \pm 11$ of S-score) (Figure 5A–C). The R-score was stable over the two periods ($54\% \pm 11$ in the 1980s and $54\% \pm 15$ in the 2020s) (Figure 5D).

Using the elbow inflection point method on the AUC, the first four dimensions of the CWM space based on the

12 traits of the 1980s and the 2020s communities were selected (68.9% of total variance explained) (Appendix S2: Figure S5). The first PCA axis opposed late and short-flowering communities to early and long-flowering communities (Appendix S2: Figure S6A, Appendix S3: Table S1). Weed communities of the 2020s were dominated by earlier and longer flowering species compared with the 1980s communities (Appendix S2: Figure S6B,C). The second PCA axis was mainly driven by soil moisture and species temperature requirements (Appendix S2: Figure S6A, Appendix S3: Table S1). Weed communities from the 2020s were composed of species with lower soil moisture requirements and were more thermophilic than the 1980s communities (Appendix S2: Figure S6B,D). The third axis of the functional space was mainly driven by SLA (Appendix S2: Figure S7A). Current weed communities were composed of species with higher SLA compared with the 1980s communities (Appendix S2: Figure S7A,C). Finally, the fourth axis was mostly driven by the percentage of C4 species within the communities (Appendix S2: Figure S7B, Appendix S3: Table S1). This axis did not significantly discriminate the 1980s from the 2020s weed communities (Appendix S2: Figure S7B,D). Many CWM correlated significantly (Appendix S3: Table S2). Flowering onset was negatively correlated with the duration of flowering ($\rho: -0.72, p < 0.001$) and positively correlated with maximum height ($\rho: 0.75, p < 0.001$). The Ellenberg indices for temperature were positively related to Ellenberg indice for light ($\rho: 0.64, p < 0.001$) (Appendix S3: Table S2).

Drivers of the shift in weed community functional and taxonomic structures between the 1980s and the 2020s

Climate change, weed management trajectory, and the 1980s and the 2020s weed management frequency were not selected in the models explaining changes in abundance and taxonomic (richness, Shannon and Pielou), phylogenetic and functional diversity indices (RaoQ) of weed communities between the 1980s and the 2020s. Most of the variance was explained by the vineyard identity effect: 31% for the changes in abundance, 61% for the changes in richness, 27% for the Shannon index and 9% for the Pielou index, 30% for trait distance-based RaoQ and 13% for phylogenetic distance-based RaoQ.

From the 1980s, season, management, and climate changes influenced the intensity of functional changes in the weed communities (Table 3, Figure 6). From the 1980s to the 2020s, the shifts in LDMC and S-scores toward higher values were more intense in vineyards that experienced a shift toward higher annual temperature ranges, thus higher climate change intensity (Table 3,

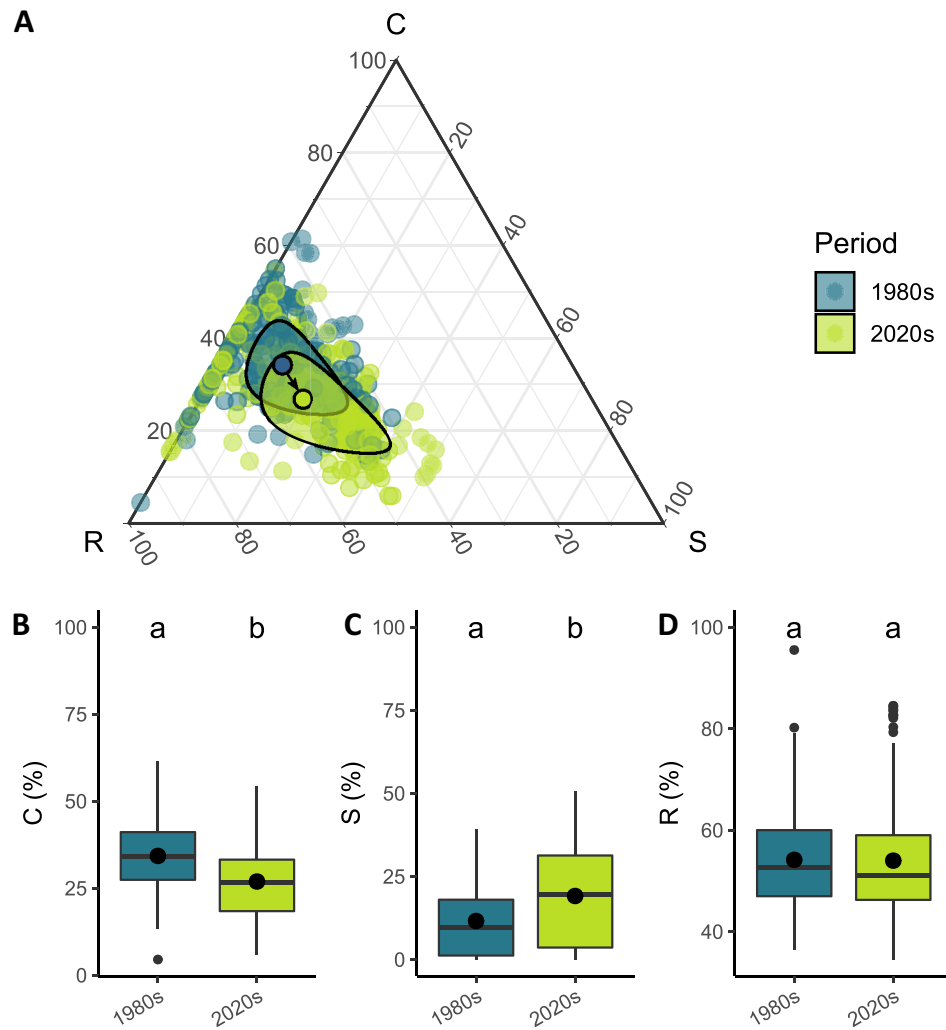


FIGURE 5 (A) Shift in CSR strategies of weed communities from the 1980s to the 2020s in Grime's triangle. Each dot is a community and their color indicates the period when the community was observed (blue, 1980s; light green, 2020s). The two dots with black outlines are the barycentres of the communities of each period and the black ellipses represent the variance in 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; R, ruderals; S, stress tolerators. $n = 374$ floristic surveys.

Figure 6A,F). Vineyards that experienced higher climate change as proxied by the shift in annual temperature ranges were composed of less ruderal weed communities (Table 3, Figure 6E). Vineyards that were managed with frequent mowing of interrows in the 2020s had more strongly shifted to lower ruderal scores (Table 3, Figure 6D). The weed communities where farmers stopped herbicide use for a long time had higher seed mass than weed communities with continuous spraying (Table 3, Figure 6B). Vineyards that were managed with more diversified practices (two or three different practices) had shifted toward a higher proportion of C4 (Figure 6C). The season of floristic surveys had a strong impact on the intensity of functional shifts. From the 1980s to 2020s, the shifts in leaf area and C and S-scores

were more intense in March than in June (Table 3). In contrast to this general trend, the proportion of C4 species increased more intensely in June than in March (Table 3).

DISCUSSION

Four main findings were highlighted in this study. First, we demonstrated that climate change occurred during the four decades of the study time scale through the increase in the annual range of temperatures and summer temperatures (Figure 7). Second, we found that weed management shifts from the 1980s to the 2020s were mostly characterized by the adoption of mowing and

TABLE 3 Standardized 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; R, ruderal tolerators).

Functional characteristics of weed communities	Explaining variables	Std. est.	SE	<i>t</i>	<i>p</i>	Marg. <i>R</i> ²	Cond. <i>R</i> ²
ΔCWM							
ΔLDMC	ΔT.Range	0.46	0.11	4.26	<0.001	0.20	0.41
ΔLeaf area	Season	-0.80	0.20	-3.93	<0.001	0.11	0.27
	Mar vs. Jun						
	Oct vs. Jun	-0.51	0.20	-2.52	0.013		
ΔSeed mass	Nb.decades.stop.Chem	0.45	0.12	3.82	<0.001	0.20	0.21
ΔC4	Season	-0.67	0.19	-3.46	0.001	0.22	0.34
	Mar vs. Jun						
	Oct vs. Jun	0.34	0.19	1.72	0.088		
	Practices_diversification	0.23	0.10	2.31	0.023		
ΔCSR strategy							
ΔC	Season	-0.97	0.20	-4.86	<0.001	0.18	0.30
	Mar vs. Jun						
	Oct vs. Jun	-0.80	0.20	-4.04	<0.001		
ΔS	Season	0.57	0.18	3.13	0.002	0.27	0.42
	Mar vs. Jun						
	Oct vs. Jun	0.50	0.18	2.73	0.007		
	ΔT.Range	0.46	0.10	4.71	<0.001		
ΔR	Nb.Mow.IR.2020	-0.38	0.13	-3.04	0.003	0.32	0.56
	ΔT.Range	-0.43	0.11	-3.96	<0.001		

Note: Significant *p*-values (*p* < 0.05) are in bold. *n* = 108. The other acronyms are detailed in Table 1. Abbreviations: Cond. *R*², conditional *R*²; LDMC, leaf dry matter content; Marg. *R*², marginal *R*²; *p*, *p*-value; Std. est., standardized estimates; *t*, *t*-value.

more frequent row chemical weeding and less frequent chemical weeding of the interrows. Third, we described major shifts in weed community: (1) higher abundance and richness and lower evenness; (2) many species (~30%) increased in abundance and frequency (e.g., *Medicago polymorpha*) while fewer (~20%) decreased (e.g., *Allium vineale*) and others remained very stable (e.g., *Lolium rigidum*); (3) CWM of SLA and LDMC increased, while CWM of leaf area, seed mass, and the proportion of C4 decreased, (4) weed communities shifted toward earlier and longer flowering, lower Ellenberg indice of soil moisture, and higher Ellenberg indice of temperature; (5) weed communities shifted toward more stress tolerance strategies and less competitive strategies.

One of the main results of this study is that weed communities from the 2020s were 41% more abundant and 24% more diverse in species than the 1980s communities at the vineyard level. In arable lands, previous studies on weed community changes over time showed drastic opposite trends: -42% to -46% in species richness from the 1970s to 2000s (Fried et al., 2016; Fried, Petit, et al., 2009) and -67% in species density (Fried, Petit,

et al., 2009). The contrasts between these studies and our results can be explained by a different temporal coverage. Indeed, the period 1970s–2000s captured the strong filtering effect of herbicide adoption in arable lands before changes in more extensive weed management practices in the 2000s (Fried, Chauvel, et al., 2009). On the contrary, the two decades from the 2000s to the 2020s captured the effect of the development of more extensive weed management. However, neither weed management practice trajectory nor climate change explained the shift in species abundance and richness. Despite the increase in richness, the functional and phylogenetic diversities of weed communities did not differ significantly from the 1980s to the 2020s. For phylogenetic diversity to be altered, a substantial introduction of new species, as well as new genera or even families, would be necessary. However, even though differences in flora are observed between the two periods, the core of the community remains relatively stable between the 1980s and the 2020s. This shows a high level of functional redundancy in the available weed species pool and the introduction of phylogenetically similar species, which maintain the overall functional and phylogenetic diversity despite

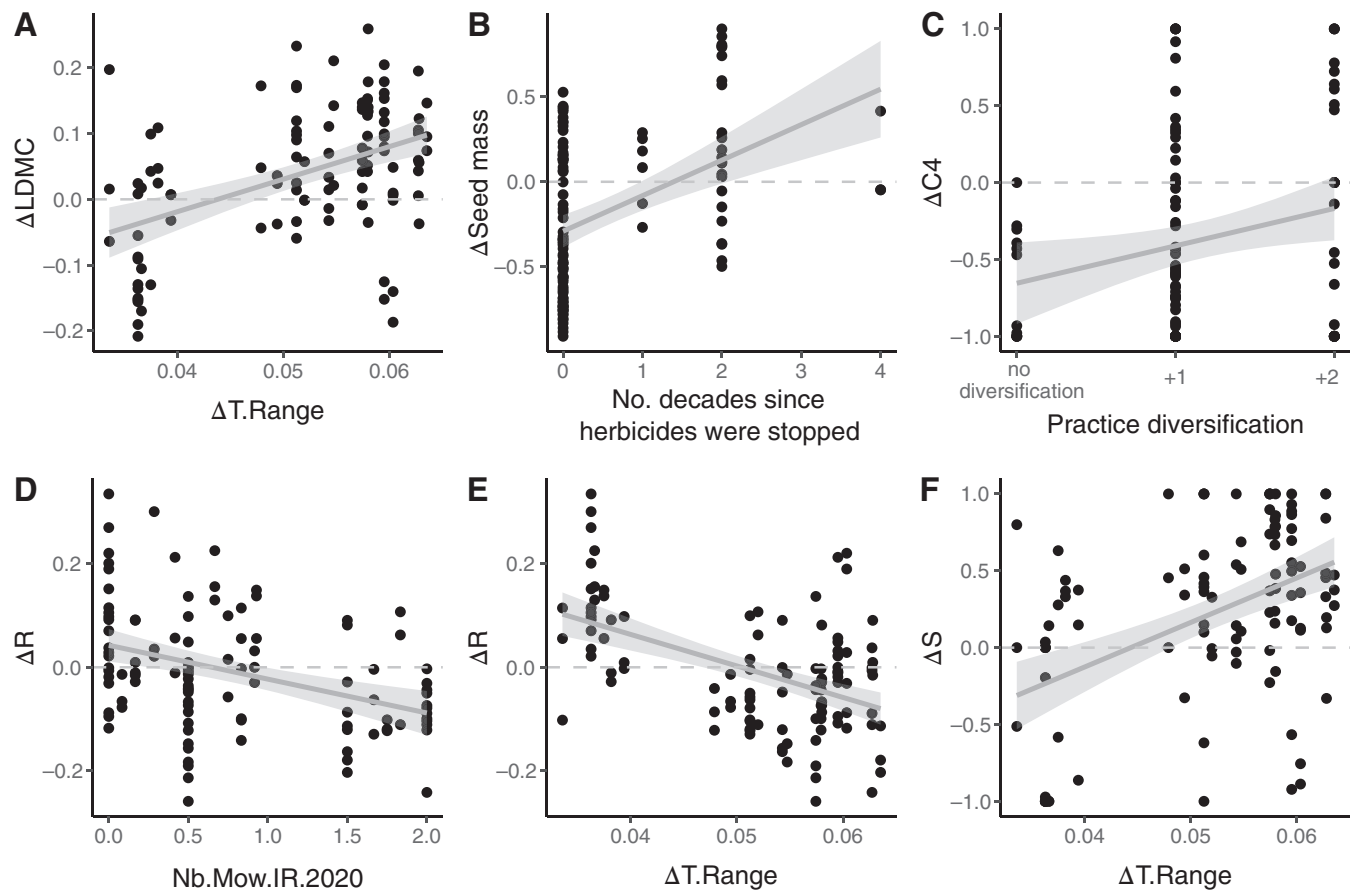


FIGURE 6 Significant effects of management and climate changes on trait shifts in weed communities from the 1980s to the 2020s. (A) Impact of the shift in annual temperature range on the changes in leaf dry matter content. (B) Effect of the timing of herbicide interruption on the changes in seed mass. (C) Impact of the practice diversification on the changes in C4 proportion within communities. Effect of the frequency of interrow mowing (D) and shift in annual temperature range (E) on the shift in R-score. (F) Impact of the shift in annual temperature range on the S-score. The acronyms are detailed in Table 1. LDMC, leaf dry matter content.

shifts in weed composition. Consequently, the ecological roles and evolutionary relationships within weed communities remained consistent.

Significant changes in climate and weed management practices over four decades

Climate shifted from the 1980s to the 2020s toward a higher summer temperature that averaged around $2^{\circ}\text{C} \pm 0.26$ and toward a higher annual range of temperatures (i.e., the difference between the warmest month's and the coldest month's mean temperatures) that averaged around 1.2°C , following the general observations trends of GIEC (Ali et al., 2022). Seasonal precipitation variability over time explained fewer climate shifts than temperature metrics from the 1980s to the 2020s. Indeed, in contrast to other regions of the world, precipitation in the Mediterranean area is projected to be quite stable (Ali et al., 2022).

We hypothesized that weed management practices would evolve toward less chemical weeding use and more frequent tillage and mowing from the 1980s to the 2020s (Cataldo et al., 2021). At large, weed management shifts matched our expectations and were driven by the adoption of mowing of the interrows that replaced to a certain extent chemical weeding of the interrows. More surprisingly, chemical weeding of rows and interrows was not widespread in 1978 and 1979 (i.e., the years of the first floristic surveys of this study) in the study sites (0.6 ± 0.5 sprayings per year) while the frequency of row spraying in the 2020s was higher (1 ± 0.8 sprayings). The use of tillage in the rows and the interrows was still frequent in 1978–1979 (9/40 vineyards). Chemical weeding spread more widely in the decade that followed the end of the 1970s, a few years after the first floristic surveys of this study. Maillet (1992) quantified for an extended group of vineyards around Montpellier (that included the vineyard group of this study) that 41% of vineyards shifted toward chemical weeding of both rows and interrows from 1979

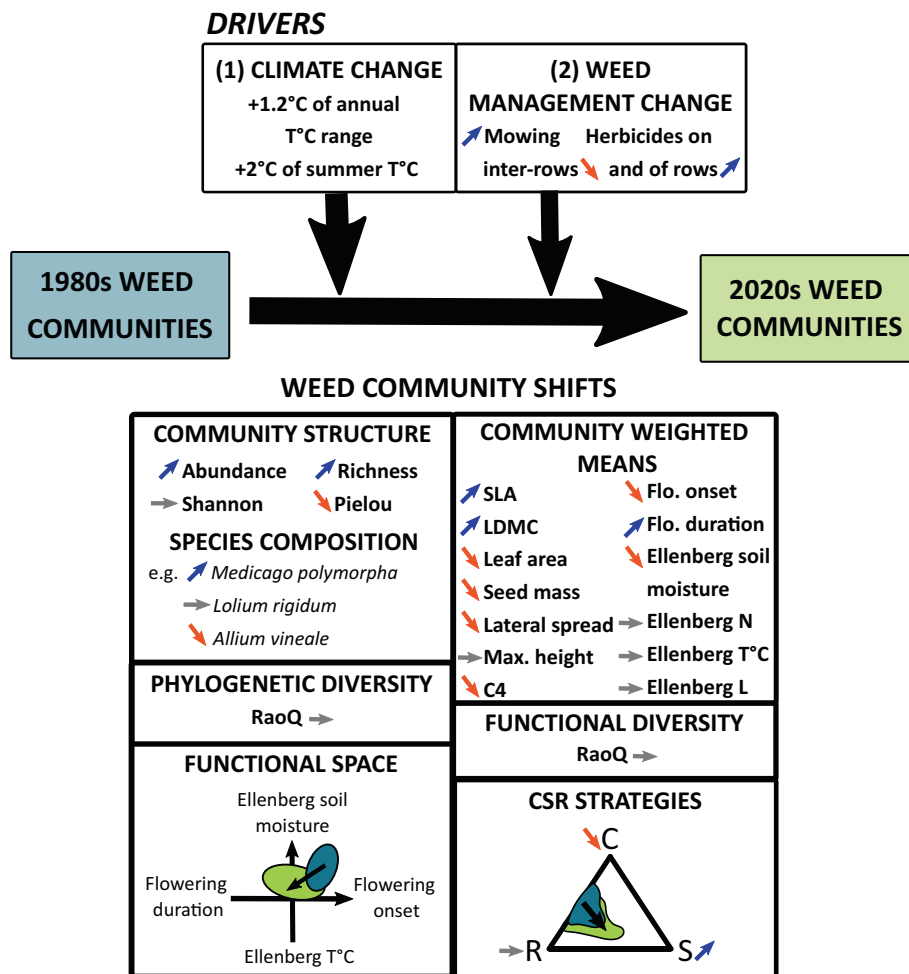


FIGURE 7 Summary of the main findings of this study. Orange arrows represent significant decreases in the variables, blue arrows represent significant increases, and gray arrows represent nonsignificant changes. Blue areas represent the functional properties of the 1980s communities while green areas represent the functional properties of 2020s communities. C, competitors; LDMC, leaf dry matter content; R, ruderals; S, stress-tolerators; SLA, specific leaf area.

to 1987. Moreover, in the 1990s, the frequency of chemical weeding increased with a second application at the end of spring to control for summer annual species, that is, species that germinate in spring and complete their cycle in summer (Maillet, 1992). In our study, we did not consider the shift in frequency of weed management and herbicide dose for the decades 1990s, 2000s, and 2010s due to the difficulty of obtaining this information from farmer interviews. In the characterization of the weed management changes, we also did not explicitly consider the active ingredients of herbicides that were different between the two periods. In the 1980s, 95% of herbicides used were simazine (pre-emergence) and aminotriazole-based (post-emergence) (Maillet, 1981). In the 2020s, herbicides were glyphosate-based (post-emergence herbicide). If the spectrum of these herbicides from both periods was broad (i.e., targeting both annuals and perennials), persistence over time is

different: simazine can persist from 3 to 15 months while aminotriazole and glyphosate persist less than one month (Maillet, 1981). Thus, in the 1980s, chemical weeding had a longer controlling action on weed communities. This, together with the fact that the area treated was often reduced to a row area in the 2020s, probably led to a reduction in the pressure of chemical weed control on the flora and could explain for instance, that even the plots that were continuously chemically weeded between the 1980s and the 2020s showed a slight increase in species richness (13%).

Climate change-induced weed community shifts toward more stress-tolerance

According to our hypothesis, at the regional scale, weed communities shifted toward more stress tolerance (+37%

for S-score). Weed communities, that shifted toward a higher score of stress tolerance from the 1980s to the 2020s, have also experienced a higher intensity of climate change (i.e., a higher increase in annual temperature range). To our knowledge, this study is the first to associate an increase in stress tolerance of weed communities with an increase in annual temperature ranges through changes in species composition. Moreover, the shifts in the annual range of temperatures were negatively associated with ruderal scores, showing that climate change might favor stress-tolerant species at the expense of ruderal species.

The increase in stress-tolerant species is related to the increase in the community-level LDMC (181 mg g^{-1} in the 1980s and 198 mg g^{-1} in the 2020s), which is the *proxy* for stress tolerance in Pierce et al. (2017). The increase in LDMC was also explained by the increase in annual range temperatures in the selected models. This indicates that climate change intensity reshuffled community composition toward more conservative species which invest in leaves with stiffer cell walls that can maintain turgidity at low water potential (i.e., more stress-tolerant) (Garnier et al., 2019). Other shifts in community-level traits indicated more conservative and stress-tolerant communities even though they were not significantly linked to the intensity of climate change. For instance, leaf area decreased over time, which has been related to a drought-tolerance strategy (de la Riva et al., 2018). Ellenberg's indice of soil moisture of weed communities also decreased significantly. Weed communities had earlier and longer flowering times in the 2020s than in the 1980s, which could also be explained by a longer growing season (Menzel et al., 2006). Surprisingly, SLA also increased while LDMC and SLA are expected to covary negatively with LDMC (Vendramini et al., 2002). As leaf area also decreased, one explanation for this pattern could be the reduction in leaf thickness, which is a component of SLA (SLA is a product of LDMC and leaf thickness) (Witkowski & Lamont, 1991). As LDMC is related to soil fertility (Hodgson et al., 2011) and leaf thickness to light intensity (Niinemets, 2001), SLA increases in response to both increased shade and increased fertility. Thus, we assumed that the observed increase in SLA is a response to increased shade in the more abundant 2020's communities (Vendramini et al., 2002). Surprisingly, the proportion of C4 species within the weed communities decreased over time while it is expected that C4 species would increase with climate change as their photosynthesis pathway is more efficient than those of C3 at higher temperatures (Heilmeyer, 2019; Peters et al., 2014). However, independent of temperature and precipitation changes, the increasing level of CO_2 , which we did not consider, has been predicted to favor C3 more than C4 (Peters et al., 2014). Indeed, C3 weeds increase their leaf

area and their biomass in higher CO_2 pressure than C4 species. Thus, they are more competitive in such conditions.

The season of the floristic surveys strongly impacted the magnitude of functional shifts of weed communities. From the 1980s to the 2020s, the shifts in leaf area, C4 proportion, and C and S-scores were more intense in March than in June. The seasonal effect, as included in the models, encompasses (1) the seasonal effect of climate changes that were not included in the summer temperature and annual temperature range shifts as well as (2) the potential seasonal shifts in practice management (i.e., timing of practices applied). An interaction between climate and practices could explain the different magnitude of shifts across seasons. Climate change might have induced earlier growth of weed communities as expected in the Mediterranean region (Gordo & Sanz, 2010), which may have led to earlier weed management to control weed–vineyard competition. However, we have no information about the date of management in the 1980s to confirm this hypothesis.

Weed management changes influenced functional shifts in weed communities

Weed management also impacted the functional shift of weed communities from the 1980s to the 2020s. Weed communities continuously sprayed with chemical weeding for four decades shifted toward lower seed mass (on average, -31% of seed mass at the community level) while those where herbicides were interrupted for more than 20 years showed the opposite trend ($+22\%$ of seed mass). As seed mass is negatively correlated to seed number (Westoby, 1998), weed community strategies under chemical control are to produce a high number of seeds to face a higher risk of seed mortality (Storkey et al., 2010). Moreover, small seeds may have higher seed dormancy (Thompson et al., 1993) leading to a lower depletion of the seed bank.

Frequently mowed weed communities in the 2020s were composed of fewer ruderal species compared to communities with different management (i.e., tillage and/or herbicides). These results are in line with those of Fried et al. (2022) and Guerra et al. (2021) that showed that mowing favored less ruderal weed communities compared with tillage in vineyards, due to a higher proportion of hemicryptophytes. Mowing is a disturbance with a lower intensity than tillage (Hall et al., 2020). Indeed, mowing destroys weed biomass partially and is generally applied later compared with the other management types (on average in May–June in our dataset vs. March–April for tillage and herbicide spraying in the 2020s). Interestingly, mowing has been shown to favor

either competitive species in regions with continental climate (Fried et al., 2022) or stress-tolerant species in Mediterranean regions (Guerra et al., 2021). In our analysis, the increase in stress tolerance was not associated with mowing frequency in the best model. However, the second-best model included a positive effect of mowing frequency on stress-tolerance scores and the two variables correlated significantly ($\rho = 0.25$, $p = 0.01$), suggesting a small tendency that is consistent with the Guerra et al. (2021) results.

Weed management in perennial cropping systems in the context of global change

The trend toward more stress-tolerant, less competitive, and more diverse weed communities that we identified for perennial cropping systems contrasted with several studies based on annual cropping systems (Moss et al., 2004; Storkey et al., 2010). In annual cropping systems, the temporal increase in weed competitiveness was observed from 1969 to 2014 in the Broadbalk Experiment, UK, and was partly related to an increase in nitrogen input (Storkey et al., 2021). In our study, fertilization was not considered due to the difficulty in obtaining the data from farmers for the 40 years. However, fertilization amount in Mediterranean vineyards is quite low (Metay et al., 2014) and the global temporal trend in fertilization in vineyards contrasted with the trend in annual cropping systems. Indeed, vineyard fertilization has decreased over the past decades to increase wine quality (Verdenal et al., 2021), and this trend could also explain the decrease in weed community competitiveness. Weed management modulates vine water supply, which is a key determining factor of crop productivity and fruit quality (Leeuwen et al., 2009). Changes in weed management strategies (e.g., choice to sow a cover crop in the interrows) and weed management tactics (e.g., choice of the date of weed destruction) are both needed to adapt vineyard management to higher temporal uncertainty, for short- and long-term changes, in the context of climate change.

Conclusion

Weed communities have strongly shifted from the 1980s to the 2020s toward higher richness and abundance. We showed that management and climate changes are modeling functional changes in plant communities over time. The current shift toward more extensive weed management in vineyards involving mowing might be driving more diverse and abundant plant communities. We showed that the CSR framework is relevant to assessing

changes in environmental conditions along the resource gradient and shifts in management along the disturbance gradient. In response to climate change, weed communities are more stress-tolerant. The diversification of weed management techniques in the interrows based on less herbicide use and more tillage or mowing practices, at the plot level, drove less ruderal weed communities.

AUTHOR CONTRIBUTIONS

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

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Bopp et al., 2024) are available in Dryad at <https://doi.org/10.5061/dryad.sn02v6xcr>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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