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Abstract

Vineyards are an appropriate model for testing the filtering effect of management practices on weed communities, as a wide range of practices (tillage, herbicides and mowing) is implemented. The aim of this study is to highlight which trait values are selected by each practice in different environmental conditions, with special references to Grime's CSR strategies. A combination of a multivariate analysis (RLQ) and the fourth-corner analysis was used to analyse 400 floristic samples belonging to 100 vineyards in the wine-growing region of Bordeaux (France). The main structure of vineyard weed communities was shaped by the opposition between mowing, favouring hemicryptophytes with a competitive strategy, and soil tillage, favouring therophytes and nutrient-demanding species with a ruderal strategy. Secondly, the vineyard weed communities differed according to the trophic status of the soil. Vineyards on acidic, sandy soils with low organic matter were characterised by small-seeded annuals with a stress-tolerant strategy whereas vineyards with clayey, calcareous soils rich in organic matter, harboured larger perennial nitrophilous species with large seeds and a competitive strategy. Our study is the first to show that weed species responded consistently to two independent gradients with specific traits associated with disturbance (life cycle and SLA) and soil resources (plant height and seed mass) gradients. Based on knowledge of the soil characteristics, it becomes possible to predict which type of weeds will develop according to the combination of practices applied on the vineyard rows and inter-rows.

KEYWORDS
functional ecology, herbicides, management practices, mowing, response traits, tillage, vine, weed communities

1 | INTRODUCTION

Since Booth and Swanton's seminal article (Booth & Swanton, 2002), there have been a large number of research studies using a trait-based approach that aimed to identify general rules explaining the effect of agricultural practices on arable weed communities (Fried et al., 2009b; Gunton et al., 2011; Ryan et al., 2010; Trichard et al., 2013). In this framework, agricultural practices are considered as filters that reduce the probability of presence of species that do not have suitable trait values, progressively replaced by more adapted weed species (Booth & Swanton, 2002; Fried et al., 2009b). Weed community responses to particular practices, such as tillage, have been examined mostly in annual crops (Armengot et al., 2016; Plaza et al., 2015; Zanin et al., 1997). No-till systems have been shown to favour weed communities with more perennial plants, small plants with great affinity for nutrient-rich soils, flowering later in season and producing a high number of small seeds compared to those observed in conventional tillage systems (Armengot et al., 2016). From a functional point of view, the effect of herbicides on weed communities has been less studied, although it was shown that herbicides selected for late-emerging weed species whose life cycle avoid the herbicide filter (Fried et al., 2012; Gulden et al., 2010). The effect of fertilisation has been even less investigated (but see Cordeau et al. (2021)) even if diachronic studies suggested indirectly that increased amount of N-fertilisation can favour nitrophilous weeds (Fried et al., 2009a).

Highlighting the role of management practices on the assembly of weed species into communities is challenged by the interaction between practices coherently implemented by farmers, and the interaction between practices and the environmental abiotic conditions (e.g., the effect of fertilisation can be hindered by the effect of the natural soil fertility). One option is to experiment and control for different factors in experimental farms (see e.g., Ryan et al. [2010]). However, even if a trait-based approach sheds light on filtering mechanisms, conclusions of experiments remain strongly limited to local conditions (e.g., soil type, weather and species pool). To overcome these limitations, the analysis of large-scale weed surveys covering wide gradients of disturbance (generated by farming practices) and environmental factors (available resources and climate) is required. Indeed, Gaba et al. (2014) suggested that the effects of cropping systems on the environment can be summarised into disturbance and resource gradients with distinct plant traits responding to each component of the two gradients. According to Grime's CSR strategies (Grime, 1974, 1977; Pierce et al., 2017), distinct plant strategies should be observed along these two gradients with competitive species (C) in the more productive and less disturbed fields, ruderal species (R) in the more disturbed fields and stress-tolerant (S) in the less productive and less disturbed fields. So far, even if the application of CSR strategies has largely been used for managed grasslands (Moog et al., 2005), few studies have tested if these strategies responded to agricultural disturbance and resource gradient in vineyards.

The response of weed communities to farming practices through a functional approach has been extensively studied in annual field crops (for a review, see Gaba et al. [2017]). However, weeds and crops grow in fertile environments and weeds are often managed with herbicides, reducing the length of disturbance and resource gradients explored. Conversely, the grapevine is a more relevant and understudied system for analysing the link between agricultural practices and weed trait values. First, at the regional scale, management practices in vineyards are very diversified (including combinations of tillage, mowing and herbicides) and vines are planted in a very varied context of soil resources (including on dry hillsides or on poor sandy or stony soils), generating larger gradients than annual crop fields both in terms of disturbance and resources. Second, at the vineyard scale, distinct management practices are usually applied on the rows and inter-rows of the crop. For example, in an increasing number of vine regions, the inter-rows are mowed or tilled while only the rows are sprayed with herbicides. Additionally, as vineyards are permanent crops, practices are less likely to change from year to year as in traditional crop rotation, thus allowing patterns to emerge (i.e., correlation between species and practices).

Previous studies on weed communities in vineyards have shown that management practices can influence weed community composition and diversity (Fried et al., 2019; Gago et al., 2007; Lososová et al., 2003). Weed diversity and abundance generally decrease as tillage or herbicide use increases, while mowing leads to richer communities with more abundant species (Fried et al., 2019; Kazakou et al., 2016). Different management practices (tillage vs. herbicides) also lead to particular species assemblages, suggesting a different filtering effect (Fried et al., 2019). From these taxonomic studies, it was already established that annuals are generally favoured in tilled/sprayed vineyards, while mowing allows the survival of perennials. However, due to the high diversity of species found in vineyards (e.g., around 900 species in France [Maillet, 2006]), taxonomic approaches have failed to highlight consistent responses of weeds to management practices. More recently, an increasing number of studies have investigated the response of weed communities to vineyard management, using a trait-based approach (Bopp et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; MacLaren et al., 2019; Mainardis et al., 2020). MacLaren et al. (2019) showed that herbicide-treated sites promoted relatively tall, small-seeded weeds, indicators of a ruderal-competitive life strategy. Kazakou et al. (2016) and MacLaren et al. (2019) highlighted that tillage favoured ruderal species with high SLA (specific leaf area). However, the effect of mowings showed contrasted results, promoting either shorter (MacLaren et al., 2019) or taller weeds (Bopp et al., 2022; Kazakou et al., 2016; Mainardis et al., 2020), so lacking a totally clear signal on the selected Grime strategy. One possible reason for these mixed results regarding Grime strategies is that these studies either considered only the inter-rows (Hall et al., 2020; Kazakou et al., 2016), only the rows (Mainardis et al., 2020) or used samples that indistinctly cover the vegetation over both rows and inter-rows (MacLaren et al., 2019). As management practices can be very contrasting between the inter-rows and the rows (typically, herbicides sprayed on the rows, mowing in the inter-rows), distinct weed surveys on these two areas may allow to disentangle more easily the effect of the environment (climate and soil) from the effects of the practices. Another limitation of these studies is that they do not explicitly take into account the resource gradient, except for Guerra et al. (2021) who

show that irrigation favours taller and more competitive species. We expected that tillage and herbicide would favour ruderal communities while mowing would select more perennial communities. Indeed, tilled and sprayed vineyards both experience disturbance of high intensity that destroy all the vegetation biomass while mowing removes it partially. Taking into account the soil richness gradient and fertilisation, we also hypothesise that regardless of management practices, vineyards on fertile and/or fertilised soils will favour competitive species and vines with poor resources (sandy texture and low organic matter) and/or low fertilisation will favour stress-tolerant species.

Additionally, landscape data can help understand how the land cover around the studied vineyards influences weed community composition or diversity in the vineyards (Hall et al., 2020). Many studies have examined local plant diversity as a function of habitat-specific communities in a mosaic landscape (Honnay et al., 2003; Wagner et al., 2000) and some supported the hypothesis that local plant species richness in arable fields is influenced by processes operating at the landscape scale (Gabriel et al., 2005). However, much fewer studies have considered the landscape filtering effects on traits, for example, on dispersal which is a major landscape-level ecological process (Duflot et al., 2014).

The objective of the study is: (1) to characterise the agro-environmental gradient of the vineyards (in a disturbance and resource gradient), (2) to identify the response trait values of the species along these two gradients and (3) to test if the Grime's CSR strategies of the species are selected by the resource and disturbance gradients. In accordance with the literature discussed above, we hypothesised that distinct management practices will select specific functional types of weeds (those possessing the requisite trait values to pass through the filters) and that Grime's CSR strategies can summarise these along the disturbance and the resource gradients.

2 | MATERIALS AND METHODS

2.1 | Study area and vegetation surveys

Plant communities, management practices and environmental variables were surveyed in the Bordeaux wine-growing region (South-West of France), one of the world's most famous wine regions although the second in size after the Languedoc wine region. Floristic surveys were performed during spring and summer 2015 in 100 vineyards mostly distributed in the Gironde department (Figure 1A,B). In each vineyard surveyed, the sampling area covered two distinct rows and four distinct inter-rows (Figure 1Cs). For each of these six plots, sampling consisted in the identification of the flora (presence and abundance of species) over a length of 25 m and a width of 1 m, which corresponded to a total of 150 m^2 per vineyard (Figure 1C). Abundance was estimated based on the cover percentage of each species per plot. The sampled rows (R) and the inter-rows (IR) of each vineyard were randomly chosen. Potential edge effects were avoided by locating the surveyed area beyond two stakes from the edge (i.e., around 10 m). In each area, vegetation was recorded twice: first at the end of March/beginning of April,

that is, before the first vegetation management (i.e., herbicides, tillage and mowing) were applied in the vineyard; second, at the end of June/beginning of July, that is, after all management practices have been applied. We performed 400 vegetation surveys describing vegetation in the rows in spring (100 samples) and in summer (100 samples) as well as vegetation in the inter-rows in spring (100 samples) and in summer (100 samples).

2.2 | Environmental variables and management practices

Climatic conditions were summarised by the annual mean temperature, mean rainfall and mean potential evapotranspiration of the year 2015 based on the data of the TRYDEA tool (French Institute of Wine and Vineyards, Table 1). Soil was sampled at two depths: 0–30 and 30–60 cm, using an auger. On each vineyard, six auger samples were taken on two inter-rows of the vineyards and six others on two rows of the vineyards in the same area where the vegetation was surveyed. The samples were pooled to have one soil analysis per surveyed vineyard. The analyses were performed by the AUREA laboratory based in Blanquefort (Gironde, France) and included: Clay/Silt/Sand percentages, Calcareous content, Organic matter content, Carbon/Nitrogen ratio, pH measured with water, pH measured with KCl, Cation exchange capacity, P_2O_5 content, K_2O content, MgO content. As several soil variables were correlated, we performed a Principal Component Analysis (PCA) and kept the first three axes, which represented 66% of the inertia and represented the percentage of sand (PCA axis 1), organic matter content (PCA axis 2) and Calcium carbonate content ($CaCO_3$) (see Figure S1). We considered that the soil nutrient gradient is positively related to organic matter content and negatively related to sandy texture.

The landscape database had been obtained in a previous study (Boisson, 2016) that characterised the landscape in a 100 m buffer zone around the vineyard with the proportion and the area of each land cover type (urban zones, annual crops, perennial crops, bodies of water, grasslands, vineyards, forests and woodlands, as well as a miscellaneous category). After performing a PCA on all the 19 landscape variables (not shown), we decided to summarise landscape metrics by the percentage of vineyard area in the buffer zone (negatively correlated with the Shannon diversity index of land cover types). This variable represented the homogeneity of the landscape surrounding the studied vineyards (i.e., low values mean high heterogeneity of the landscapes with hedges, grasslands and other types of land uses, while high values mean mainly other vineyards around the studied vineyards).

The management practices applied in the vineyards were collected through an interview of the winegrowers involved. Management practices were summarised by the number of soil tillage in the rows (till_r) and inter-rows (till_ir), the number of mowings in the rows (mow_r) and the inter-rows (mow_ir), and the number of herbicide treatments (applied at the recommended dose), the latter always being applied in the rows only (herbi_r). The number of applications of fertiliser (chemical or organic) and the total number of tractor passes
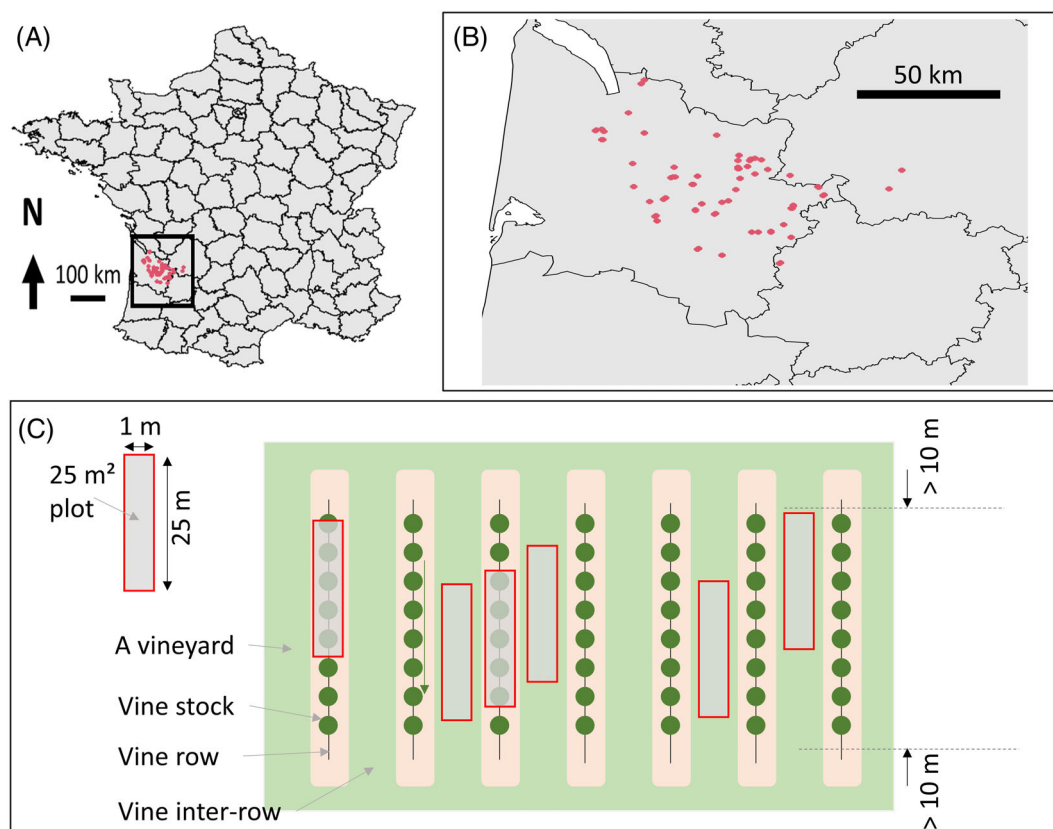
FIGURE 1 Location of the sampled vineyards (red dots, $N = 100$) (A) in Southwestern France and (B) in the Gironde department. (C) Illustration of the sampling protocol per vineyard.

(including fungicide treatments, harvesting, etc.) were also included. This latter variable is the sum of the number of tractor passes which is an indirect measurement of soil compaction. In 2016, the dominant model of management practices in the Bordeaux wine region corresponded to chemical weed control in the rows (1.8 treatments on average), coupled with mechanical weed control in the inter-rows with an average of 1.9 tillage operations and 2.1 mowing (based on Simonovici [2019], see Table 1 for comparison with the studied network). Vegetation cover in the inter-row was present in 84% of Bordeaux vineyards (92% in our network). Most of the time, it was a permanent cover of spontaneous vegetation (75%), more rarely a permanent (6%) or temporary (3%) sown cover crop. Organic farming was implemented in 11.6% of the Bordeaux vineyards (compared to 40% in our network). Table 1 gives the range (min/max), mean values and standard deviation of all environmental, landscape and management variables. This indicates the assumed link between traits and variables plus disturbance and resource gradients.

2.3 | Plant traits and Grime's CSR strategies

Five traits were selected and summarised in Table 1. Maximum plant height at maturity represents the ability to compete for light with neighbouring plants (Westoby et al., 2002). SLA represents the ability to acquire and use resources during the favourable period, and is positively correlated to the relative growth rate of weed seedlings (Storkey, 2004). Flowering phenology (onset and period) is a key trait in disturbed habitats (Gaba et al., 2017). An early flowering period is usually associated with fast-growing and small-statured species. These early emerging species, with early flowering onset and short life cycle, are expected to better escape management practices, because they can produce seeds before the first vegetation management occurring at the end of March (Gaba et al., 2017). High seed production (often associated with low seed mass) can indicate a greater seed bank and counterbalance high mortality rates due to herbicide applications (Storkey et al., 2010). In addition to these five traits, we also used Raunkiaer's life forms assuming that therophytes and geophytes are more adapted to disturbance than hemicryptophytes and woody species. Finally, the Ellenberg indicator value for nitrogen (Ellenberg-N) was considered as a synthetic nutrient requirement trait. Increasing rates of fertilisation in arable fields have been shown to favour nitrogen-demanding species (Cordeau et al., 2021; Fried et al., 2009a, 2009b). In the following analyses, plant height and seed mass were log-transformed to ensure normality.

In addition, we also used Grime's classification of plants in the CSR strategies (Grime, 1977; Hodgson et al., 1999) as a supplementary grouping of species (not influencing the analysis). Our list of 200 species fall into seven categories: C (35 species), S (7 species), R (58 species), CR (32 species), CS (8 species), SR (15 species) and CSR (40 species). Five species were not assigned to any group.

TABLE 1 List of environmental variables (climate and soil characteristics), management practices and selected traits with their abbreviations, units, basic statistics and their coordinates on the first two RLQ axes of the global analysis. For the soil variables, the means, standard deviation and ranges refer to the main variables influencing the PCA axes (more informative than the values of the PCA coordinates). The disturbance and resource gradient column gives the expected relationships (−: Negative, +: Positive) of variables and traits with these two gradients

Climate, soil, management practices and traits, and unit	Abbreviation	Disturbance (D) and resource (R) gradient	Mean ± SD or number	Range (min–Max)	RLQ axis 1	RLQ axis 2	Sources
Temperature (°C)		R (+)	12.5 ± 1.2	10.3–14.1	0.07	−0.17	TRYDEA
Rainfall (mm)		R (+)	675 ± 47	594–849	0.08	−0.03	TRYDEA
PCA Soil Axis 1 Sand (%)	Sand	R (−)	47.8 ± 23.5	3–87.2	0.28	0.72	Soil analysis
PCA Soil Axis 2 Organic matter	Org mat	R (+)	1.8 ± 0.8	0.4–4.6	0.08	−0.34	Soil analysis
PCA Soil Axis 3 [CaCO3]	Calc	R (+)	34.2 ± 71.6	0–271	0.27	−0.49	Soil analysis
Percentage of vineyard	V_100m		77.3 ± 17.3	29.4–100	0.08	−0.08	Boisson (2016)
No. of mineral fertilisation in the last 5 years	feng	R (+)	2.1 ± 2.1	0–5	−0.04	0.14	Interview with farmers
No. of organic fertilisation in the last 5 years	famo	R (+)	6.5 ± 2.4	0–13	0.15	0.08	Interview with farmers
No. of herbicide treatments	nherb	D (+)	0.9 ± 1.1	0–3	−0.10	0.13	Interview with farmers
No. of tillage on the inter-rows (till_ir)	till_ir	D (+)	1.8 ± 1.7	0–8	0.58	0.04	Interview with farmers
No. of tillage on the rows	till_r	D (+)	2.2 ± 2.4	0–8	0.45	−0.01	Interview with farmers
No. of mowings on the inter-rows	mow_ir	D (−)	3.5 ± 1.8	0–7	−0.29	0.08	Interview with farmers
No. of mowings on the rows	Mow_r	D (−)	0.6 ± 1.4	0–5	−0.21	−0.14	Interview with farmers
Total number of mechanical passes	npm	D (+)	26.7 ± 5.4	15–40	0.35	−0.12	Interview with farmers
Raunkiær life forms							baseflor (Julve, 1998)
Therophytes	Thero	D (+)	$n = 98$	–	0.85	0.07	
Biennials	Bis		$n = 9$	–	0.21	−0.49	
Geophytes	Geo	D (+)/R (+)	$n = 23$	–	0.17	−0.44	
Hemicryptophytes	Hemi	R (+)	$n = 64$	–	−1.16	0.12	
Woody species	Woody		$n = 6$	–	−1.43	−0.50	
Specific leaf area (m² kg⁻¹)	SLA	D (+)	25.49 ± 7.21	5.55–53.24	0.15	−0.03	LEDA
Maximum plant height (m)	Height	R (+)	0.91 ± 2.11	0.1–30	−0.16	−0.48	Flora Gallica
Seed mass (g)		R (+)/D (−)	3.04 ± 10.18	0.0095–120	−0.01	−0.67	SID
Month of flowering onset (months)	Flow. On.	D (−)	4.20 ± 1.57	1–8	−0.28	−0.10	baseflor (Julve, 1998)
Flowering period (months)	Flow. Per.	D (+)	5.13 ± 2.23	2–12	−0.03	0.04	baseflor (Julve, 1998)
Ellenberg indicator value for nutrient	EIV-N	R (+)/D (+)	5.78 ± 1.59	1–9	0.16	−0.52	baseflor (Julve, 1998)

2.4 | Data analysis

To identify significant relationships between the plant traits in vineyards and the environmental and management variables, we followed the framework developed by Dray et al. (2014) combining the RLQ multivariate technique (an ordination analysis) and the fourth-corner analysis (a hypothesis testing analysis). Contrary to classical unconstrained ordination analyses such as DCA or NMDS, RLQ is a constrained ordination in which the scores of both rows (samples) and columns (species) are constrained by linear combinations of predictor variables (i.e., environmental variables and traits). RLQ assigns scores to species, sites, traits and environmental variables along orthogonal axes and provides a graphical summary of the main data structures (Dolédec et al., 1996), while the fourth-corner analysis tests for associations between one trait and one environmental variable at a time

(Dray & Legendre, 2008). While the RLQ analysis does not allow identifying precisely which environmental variable acts on which trait, the fourth-corner analysis does not account for the covariation among traits or among environmental variables. The two approaches are therefore complementary.

In the main analysis, we performed RLQ, fourth-corner analysis and their combination at the scale of the 100 vineyards, merging the four samples available (rows and inter-rows, spring and summer) by using the highest abundance scores of a species in one of the four samples. Second, to detect trait-environment relationships that may only exist in certain situations, we performed a fourth-corner analysis separately on the samples of the rows (200 samples) and inter-rows (200 samples) for both seasons, including the period of observation (spring versus summer) as an explaining variable. Similarly, we analysed separately the samples of spring (200 samples) and summer

(200 samples), including the variable area, distinguishing the row and the inter-row, as an explaining variable. In the following, these subsets of the data set will be referred to collectively as subsets, or row subset, inter-row subset, spring subset or summer subset.

Both RLQ and the fourth-corner analysis use three tables: the R-table, which consists of the 100 (or 200 for the subsets) samples described by the 15 agro-environmental (and one seasonal variable (spring vs. summer) for the row and inter-row subsets and a spatial variable (row vs. inter-row) for the spring and summer subsets), the Q-table containing the 200 species described by their seven features (five traits, Raunkiaer's life forms and Ellenberg-N) and the L-table describing the floristic composition of the 100 (or 200) samples via the abundance of the 200 species. The L-table therefore is linked with the R- and the Q-tables in the analysis through common identifiers of samples or species. RLQ selects the axes that maximise the co-variance between the site scores constrained by the agro-environmental variables (the R-table) and the species scores constrained by the species traits (the Q-table). A Monte-Carlo permutation ($n = 999$) test was used to test the null hypothesis (H_0) of absence of link between the agro-environmental Table (R) and the trait Table (Q).

Thereafter, the fourth-corner statistic (Dray & Legendre, 2008) was used to test the significance of the direct trait-environment relationships on these 100 (200) samples. This method measures the link between species traits and environmental variables using either (1) a Pearson correlation coefficient r for two quantitative variables, (2) a Pearson Chi-square ($\chi2$) and G-statistic for two qualitative variables or (3) pseudo-F and a Pearson correlation coefficient r for one quantitative and one qualitative variable. A permutation model was applied to test the null hypothesis (H_0) that species are distributed independently of their preferences for environmental conditions and of their traits (using the permutation model 6 of Dray et al., 2014). We performed 49 999 permutations and used the false discovery rate method (Benjamini & Hochberg, 1995) to adjust p values for multiple testing. In the final step, we combined the two analyses by applying the fourth-corner tests directly on the outputs of RLQ analysis. This latter approach consists in testing the associations between individual traits and environmental gradients obtained from RLQ scores, and between individual environmental variables and trait syndromes obtained from RLQ scores (Dray et al., 2014).

The Grime's CSR strategies of species were also projected as supplementary individuals on the first (global) RLQ axes to assess the consistent response of these strategies on the highlighted trait-environment gradients. Significant differences between the distribution of Grime's CSR strategies on the RLQ axes were tested by a Kruskal-Wallis test followed by multiple pairwise comparisons with the Dunn test. All the statistics were run with R (Team RC, 2020) and the ade4 package (Dray & Dufour, 2007).

3 | RESULTS

A total of 200 plant species were observed across the 100 vineyards. Nine species were present in more than 90% of the vineyards: *Taraxacum officinale* (100 vineyards), *Sonchus asper* (99), *Poa annua* (97),

Senecio vulgaris (96), *Convolvulus arvensis* (95), *Veronica persica* (94), *Plantago lanceolata* (94), *Cerastium glomeratum* (91) and *Trifolium repens* (90).

3.1 | Global responses of weed communities at the vineyard scale

The first two axes of the RLQ accounted for 78.6% of the total inertia. Environment significantly influenced the distribution of species based on their trait values (Model 2, $p < 0.001$, $N = 999$ permutations of the samples) and traits significantly influenced species assemblages found in samples with given environmental conditions (Model 4, $p < 0.001$, $N = 999$ permutations of the species). RLQ axis 1 (65.6%) discriminated primarily the management practices along a disturbance gradient, while RLQ axis 2 (13.0%) was related to abiotic factors along a soil resource gradient (Figure 2A). There was a slight correlation between the amount of mineral fertilisation and RLQ axis 2 (sand content), indicating that vinegrowers with poorer soils apply more fertiliser, but fertilisation contributed poorly to RLQ axis 2 compared to soil variables.

RLQ axis 1 was positively correlated with the number of soil tillages in the R and the IR and negatively correlated with the number of mowings both in the R and the IR (Table 1 and Figure 2A). To a lesser degree, RLQ axis 1 was also positively correlated to the total number of mechanical passages but negatively correlated to the number of herbicide treatments. Regarding species features, RLQ axis 1 discriminated Raunkiær life forms. Hemicryptophytes, woody species and species with high maximum plant height and late flowering onset were negatively correlated to RLQ axis 1 (associated with mowing) and opposed to therophytes and species with high SLA (associated with tillage) (Table 1 and Figure 2B). RLQ axis 2 was positively correlated with sand percentage and negatively correlated with organic matter content and calcium carbonate content. RLQ axis 2 opposed vineyards with several herbicide applications and high use of mineral fertilisers in production areas with low temperatures versus vineyards with low chemical use in production areas with high temperatures (Table 1, Figure 2A). Regarding species traits, RLQ axis 2 discriminated traits related to competitive ability (seed mass, plant height and Ellenberg indicator value for nitrogen). RLQ axis 2 was negatively correlated with seed mass, Ellenberg indicator value for nutrients, geophytes and maximum plant heights, that is, these traits are positively correlated with more fertile soils (Table 1 and Figure 2B).

The fourth-corner analysis showed 18 significant correlations (over 154 possible, i.e., 12%) between environmental variables and traits (see correlation and p values in Figure 3). Hemicryptophytes were positively correlated with the number of mowings in the IR and negatively correlated with the number of soil tillages in the R and IR, with the number of mechanical passages as well as with the sand percentage and calcium carbonate. Conversely, therophytes were positively correlated with the number of soil tillages both in the R and IR and negatively correlated with the number of mowings in the R and IR. Therophytes were also positively correlated with the sand

FIGURE 2   Results of the first two axes of the RLQ analysis: (A) coefficients for environmental variables (blue) and traits (red), (B) scores of species. Codes for variables and traits are given in Table 1. Species names are abbreviated with EPPO codes.
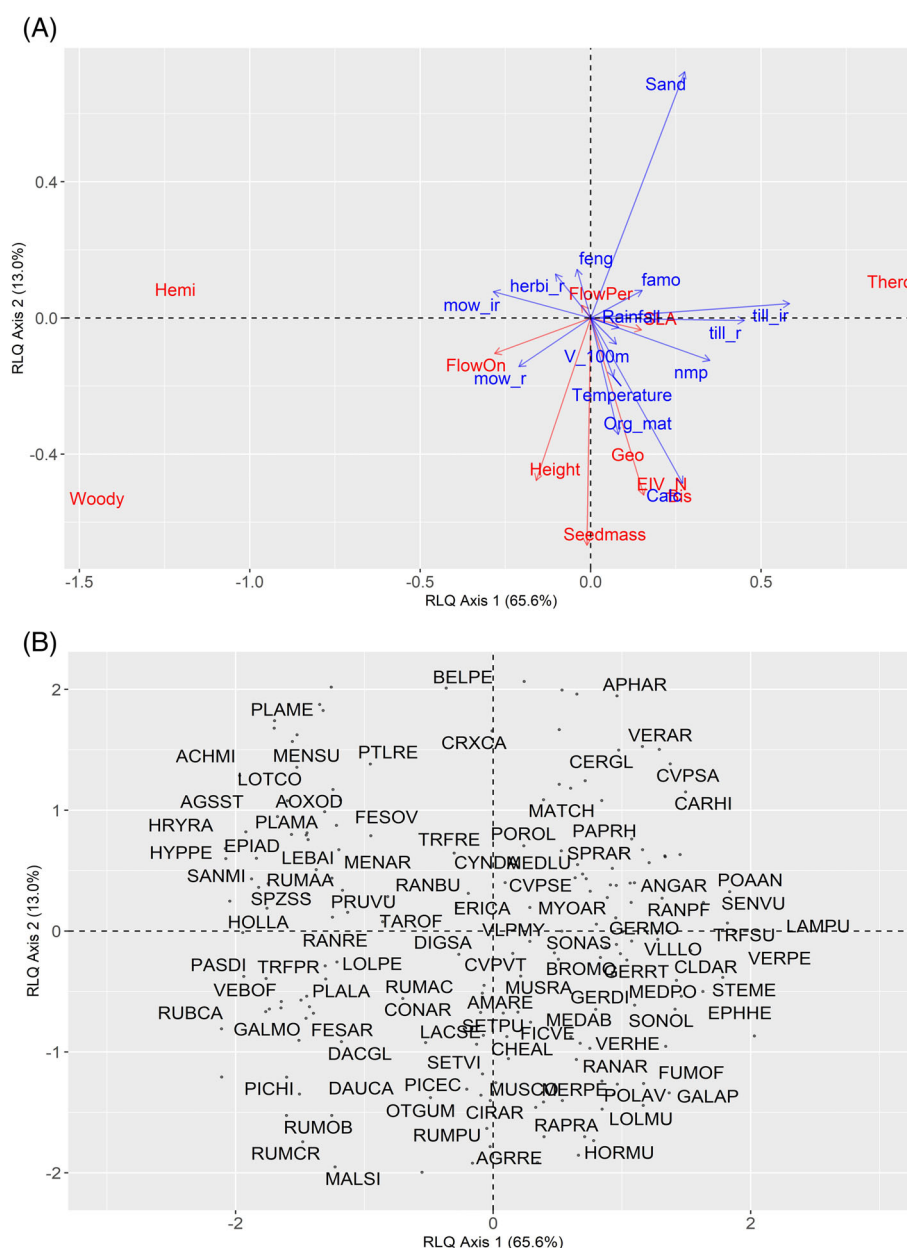
percentage and calcium carbonate content. Finally, maximum plant height and seed mass were negatively correlated with the sand percentage, and seed mass was positively correlated with calcium carbonate content and organic matter.

The combination of RLQ and fourth-corner analyses showed that early flowering annual species were positively associated with RLQ axis 1, that is, associated with soil tillage, high numbers of mechanical passages, and organic fertilisation on sandy or calcareous soils, while late flowering hemicryptophytes were negatively associated with RLQ axis 1, that is, associated with mowing (Figure 4). Species with high values of maximum height, seed mass and Ellenberg values for nitrogen were associated with RLQ axis 2, that is, positively associated with calcium carbonate content and negatively with sand percentage.

3.2 | Specific responses of weed communities at the scale of rows, inter-rows, spring or summer seasons

The results of the fourth-corner analyses with the row, inter-row, spring and summer subsets were largely similar to those obtained at the vineyard scale (presented above), in particular, the association of hemicryptophytes with mowing, therophytes with tillage and the positive association between seed mass, organic matter and calcium carbonate content in the soil (see Figure 5 for a summary of the results, Table S1 gives the detailed relationships for each subset).

However, some additional relationships were highlighted only at the scale of some or several of these subsets. The fourth-corner analyses in the R and the IR indicated a strong association between flowering onset
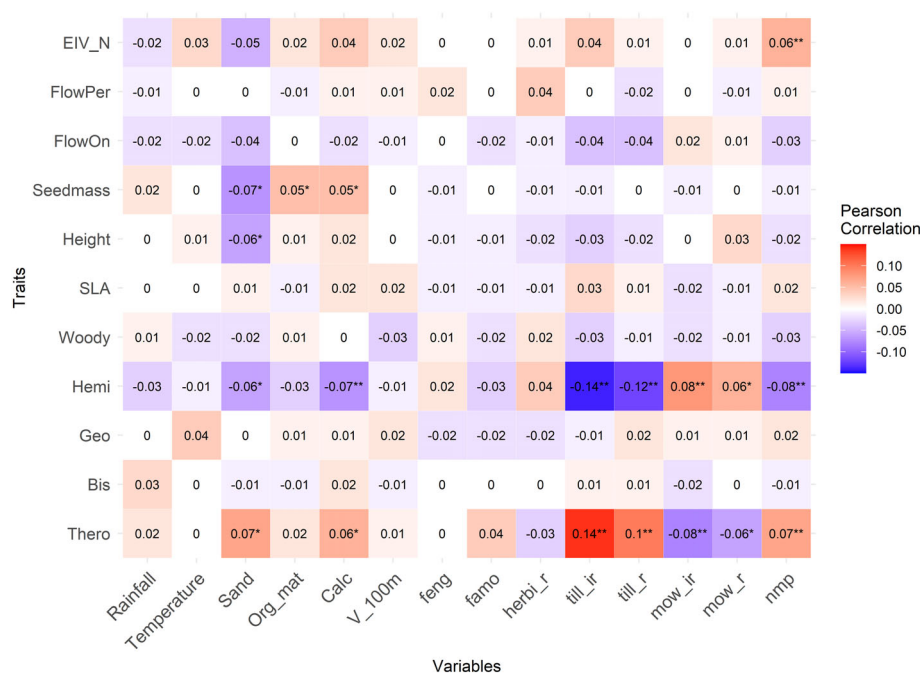
FIGURE 3 Results of the fourth-corner tests. Positive and negative associations (Pearson's correlation *r*) between environmental variables (detailed in Table 1) are in red and blue, respectively. *$p < 0.05$, **$p < 0.01$.
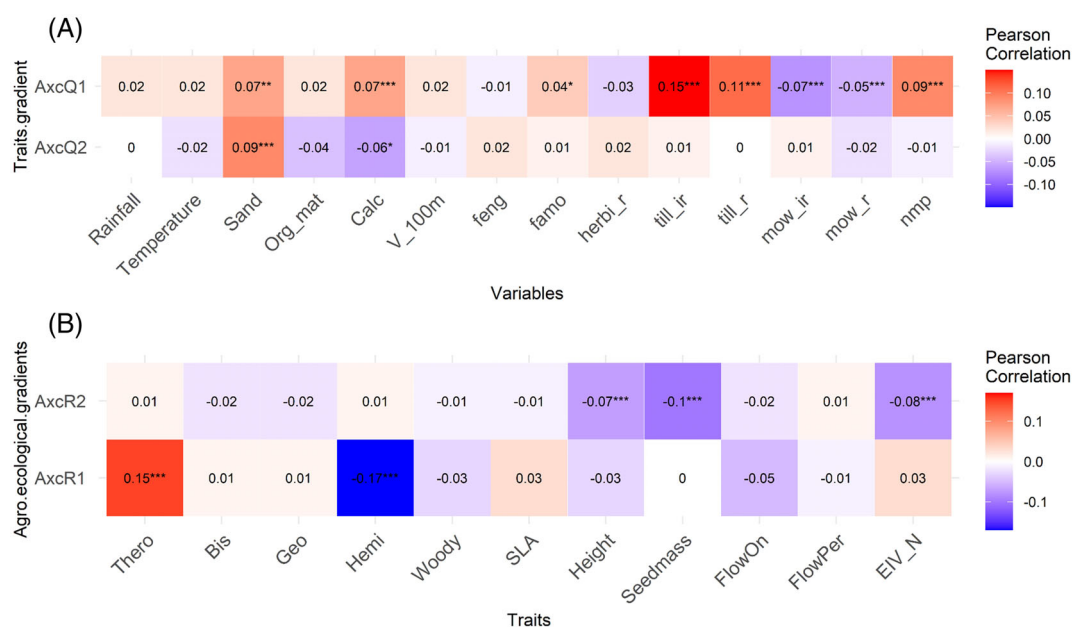
**FIGURE 4** (A) Fourth-corner tests between the first two RLQ axes (AxQ1 and AxQ2) for trait syndromes and environmental variables (detailed in Table 1). (B) Fourth-corner tests between the first two RLQ axes for environmental gradients (AxcR1/AxcR2) and traits (detailed in Table 1). Positive and negative associations (Pearson's correlation *r*) between environmental variables (detailed in Table 1) are in red and blue, respectively. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

and sampling season and also highlighted a positive link between plant height and season, that is, taller species in summer compared to spring (Figure 5). Flowering onset was also positively related to the inter-rows (and negatively related to the rows), that is, later flowering onset in the IR.

The effect of some management practices was only detected with subsets. For example, the number of herbicide applications was correlated with short early flowering species with a long flowering period when analysing the summer subset. Tillage in the IR was associated with early

flowering species (spring subset) and with species having high nutrient requirements (summer subset). Conversely, mowing on the R was related to late flowering species (spring subset). On the row dataset, the proportion of woody perennials increased with the diversity of landscape (negative relationship with percentage of vineyards in the surroundings) and with rainfall. Finally, temperature was positively related to therophytes (IR subset) and geophytes (spring subset) and negatively related to hemicryptophytes (R and IR subsets).

FIGURE 5 Number of positive (+) or negative (−) significant traits × environment relationships based on the fourth-corner analysis applied on the row, inter-row, spring and summer subsets. From light to dark red, there is 1–4 significant relationships, and from pale purple to dark blue there is 1–4 significant relationships. The detailed correlation are available in Table S1.
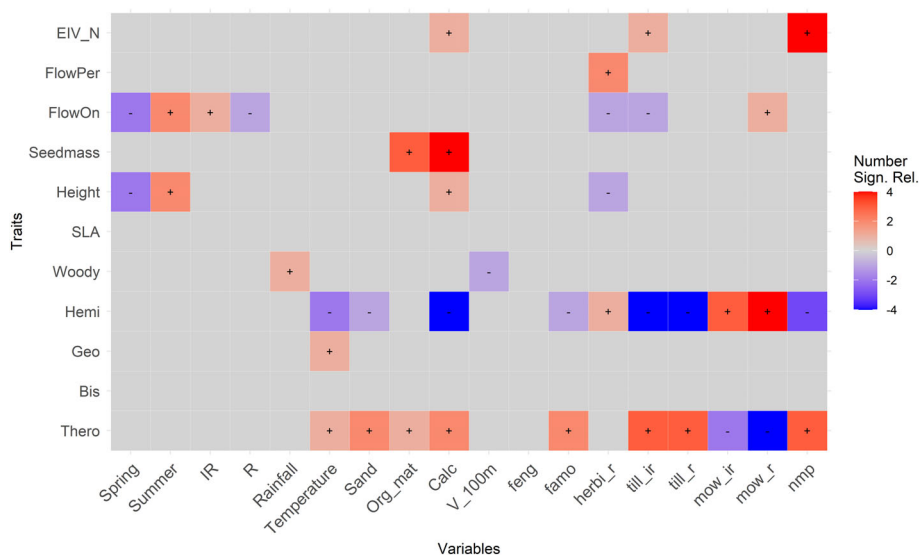
FIGURE 6 (A) Distribution of weed species according to their Grime's CSR strategies (as supplementary variable) on the RLQ axis 1 (positively correlated to soil disturbance by tillage) and (B) on the RLQ axis 2 (negatively correlated with the soil resource gradient). Different letters indicate significant differences (*p* < 0.05) based on a Dunn test.
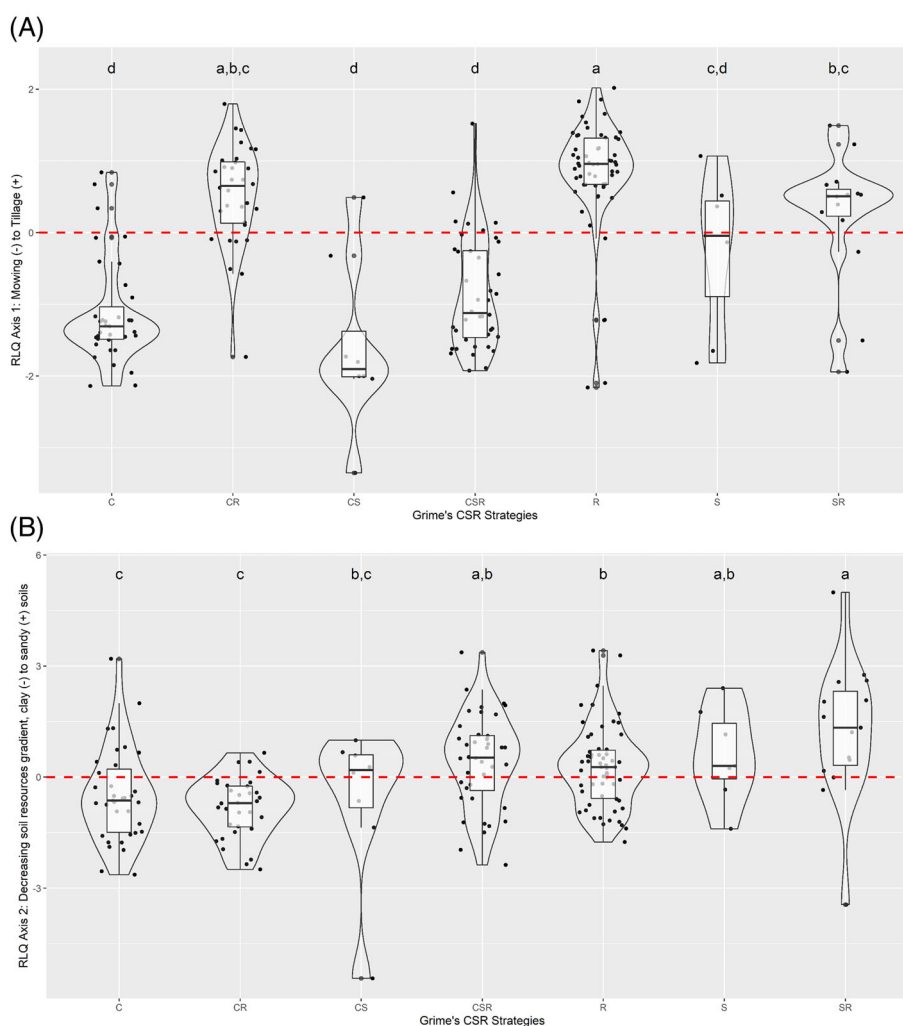
3.3 | Grime's CSR strategies in vineyards

Plotting Grime's CSR strategies as a supplementary variable on the RLQ analysis at the vineyard scale yielded in consistent results

(Figure 6). The Kruskal–Wallis test indicated significant differences in the distribution of the CSR strategies on both RLQ axis 1 (Kruskal–Wallis $X^2 = 101.74$, df = 6, *p* < 0.001) and 2 (Kruskal-Wallis $X^2 = 40.19$, df = 6, *p* < 0.001). RLQ axis 1, which expressed a soil

disturbance gradient, opposed ruderal strategies associated with tillage to competitive (C) strategies associated with mowing (Figure 5A). The mixed strategies CR and SR were associated with the R strategy while the CS and CSR strategies were associated with the C strategy. Finally, the stress-tolerant strategy (S) was located in the middle of the gradient. RLQ axis 2, which expressed a soil resource gradient, opposed C and CR strategies on clay soils with high organic matter and calcium carbonate content to S and SR strategies on sandy acidic soils with low organic matter. CS, CSR and R strategies were in the middle of the gradient.

4 | DISCUSSION

Our results highlighted a strong functional differentiation of vineyard weed communities along two orthogonal disturbance and resource gradients. Among the management practices, the opposition between tilled and mowed vineyards, which reflects a gradient of soil disturbance, supports most of the variation in weed communities. Surprisingly, the type and level of fertilisation and herbicide use had little influence although herbicides have some effect on species traits in the summer surveys. Large-scale environmental variables, such as climatic conditions and landscape diversity, also have little influence. The small effect of landscape can be explained by the fact that our plots were globally located in vine-dominated landscapes with rather small variations. This contrasts with the strong influence of soil variables, especially along a resource gradient, from acidic sandy soils to clay soils with alkaline pH and higher organic matter content. We highlighted that specific trait values were associated with these disturbance and resource gradients, reflecting consistently the Grime's CSR strategies.

Our approach combined a global analysis at the vineyard scale (combining rows and inter-rows, and the two sampling dates) and separate analyses on the subsets of row versus inter-row flora on the one hand, and on the subsets of spring versus summer flora on the other hand. As expected, while the main associations between traits and agro-environmental variables were the same with all data sets, some effects were only detected in some subsets. The main gradient in both the rows and inter-rows was the opposition between spring and summer samplings as already highlighted in a previous study of vineyard weed communities (Fried et al., 2019). In the same vineyards, there is a turnover between small early flowering species in spring (*A. thaliana*, *C. glomeratum*, *Crepis sancta*, *Mibora minima* and *Muscari neglectum*) replaced by tall and late flowering species in summer (*Chenopodium album*, *Daucus carota* and *Erigeron canadensis*). The effect of some variables was only detected in the rows (e.g., herbicides or landscape diversity) or in the inter-rows (organic fertilisation and temperature). This was partly due to the specific location and timing of these agricultural practices: herbicides are sprayed in spring on the rows (see below *Disturbance gradients*) and organic fertilisation is mainly applied on the inter-rows. In diversified landscapes, woody species, surely spreading from neighbouring wood patches were found on the rows but not the inter-rows. This can be explained by the greater difficulty

of management on the row where tillage cannot be as efficient as it is on the inter-row and the use of herbicide at the registered rate does not eliminate woody species. The mechanical resistance of the perennial herbaceous inter-row to colonisation may also explain this pattern, while the row is always tilled or sprayed and species colonisation is therefore favoured by suppressing physical barriers and potential competitors. More surprisingly, some practices applied in the inter-rows (i.e., tillage) also showed a correlation with species traits of the rows. This might suggest that management on one area can influence the flora in the neighbouring area (either tillage in the inter-rows creates micro-disturbances in the rows, or species favoured by tillage on the inter-rows can spread to the rows) (Boinot et al., 2019).

4.1 | Disturbance gradients

The strongest structuring factors of the weed communities of the Bordeaux vineyards was the opposition between the tilled areas (inter-rows or rows) favouring annual species with a ruderal or a competitive-ruderal strategy and the mowed areas (inter-rows or rows) with hemicryptophytes with different types of competitive strategies (C, CS or CSR). Tilled areas were dominated by species such as *Lamium purpureum*, *S. vulgaris*, *P. annua*, *Stellaria media* and *V. persica* in spring, replaced by *Amaranthus retroflexus*, *Echinochloa crus-galli*, *Lactuca serriola* and *Setaria viridis* in summer. This result is consistent with other trait-based studies conducted in vineyards with either more annuals in tilled vineyards (Mainardis et al., 2020) or more R-strategist species on bare soils (including either tillage or herbicide treatments) (Hall et al., 2020). In line with this R-strategy, we also found a link between tillage and early flowering species (i.e., rapid life cycle) and high nutrient demand. To a lesser extent, the RLQ analysis suggested that SLA was also related to the soil tillage gradient. Weed communities with high SLA values were previously reported to be associated with vineyards with bare soils, either tilled or sprayed with herbicides (Hall et al., 2020). In fact, high SLA, which is positively correlated with relative growth rate, relates to a community with rapid completion of life cycle, well adapted to highly disturbed environment. At the vineyard scale, the number of herbicides treatment did not impact communities, probably because herbicide is applied on the row only and the row area represents a minor part of the field area. However, when looking at the row scale and in the summer samplings, we found that a higher number of herbicide treatments favoured small annuals with early flowering and a long flowering period. The fact that more relationships between herbicides and species traits were highlighted in summer is consistent with the fact that herbicides are applied in April after the first survey, so the species have been filtered out by this spring treatment only in the summer surveys. This illustrates the importance of positioning and utilising weed surveys appropriately according to the studied practices (Colbach et al., 2020). In our study, flowering period was measured at the species level, that is, it corresponds to species with successive cohorts with a rapid life cycle (*Capsella bursa-pastoris*, *Euphorbia helioscopia*, *P. annua* and *S. vulgaris*). The positive link between herbicides and flowering period

can be seen as a strategy to avoid herbicide pressure, a part of the population being able to complete its cycle between two treatments. On the opposite side of the gradient, mowing favoured hemicryptophytes with different kinds of competitive strategies (C, CS and CSR). Mowed areas are dominated by *Trifolium pratense*, *Lolium perenne*, *Dactylis glomerata*, *P. lanceolata* or *Poterium sanguisoba*. It has been shown that C- and CSR-strategists were associated with permanent vegetation cover in vineyards at the European scale (Hall et al., 2020), and other studies found that cover crops and/or mowing was associated with more conservative strategies with lower SLA (Kazakou et al., 2016), higher leaf area, deeper root depths index (Mainardis et al., 2020) and taller plant size (Kazakou et al., 2016; Mainardis et al., 2020). In our study, we did not take into account sown cover crops, as they were only temporary (winter), and were destroyed by tillage. Therefore, in spring, these inter-rows look much more like tilled inter-rows (with almost bare soil) than inter-rows with permanent vegetation managed by mowing.

4.2 | Resource gradient

Contrary to our initial expectations, the number of fertilisations or amendments was not associated with more nitrophilous species (Ellenberg-N) or species with rapid resource acquisition (high SLA values). Apart from a low positive correlation between organic amendments and annual species in the inter-rows and summer subsets, there was no effect of nutrient input. In our data set, it seems that the soil fertility gradient was more related to the soil characteristics opposing sandy acidic poor soils to clay alkaline richer soils. Interestingly, we found that seed mass, maximum plant height and Ellenberg-N to a lesser extent, were positively associated with the level of soil resource. The positive association of seed mass to soil fertility is a pattern that has been observed several times previously in natural habitats (May et al., 2013; Santini et al., 2017). DeMalach et al. (2019) demonstrated experimentally that the underlying mechanisms could be as follows: under low soil fertility (here sandy acidic soils), belowground competition is the dominant process shaping community structure. As belowground competition is size-symmetric, the growth rate advantage of small-seeded species results into higher fecundity and consequently, small-seeded species dominate the community. In contrast, under high soil fertility (here on alkaline clay soils), the dominant process determining relative growth rate becomes size-asymmetric competition for light. In such fertile soils, large-seeded species start with an initial size advantage, which further increases with time since they capture most of the light. Under these conditions, large-seeded species suppress the growth of the small-seeded species, grow faster, produce more seeds per individual and dominate the community. This mechanism is consistent with the results of our study where large-seeded species on fertile soils where also tall species with high Ellenberg-N values conferring a high competitive ability (e.g., *Elytrigia repens*, *Malva sylvestris* and *Rumex* spp.).

To summarise, the effect of tillage is very consistent across studies, and we confirmed here that tillage favoured species with a ruderal

strategy, an annual life cycle (Guerra et al., 2021; Hall et al., 2020; Mainardis et al., 2020) and an early flowering onset (Bopp et al., 2022; Guerra et al., 2021). The picture is more mixed for herbicides and mowing suggesting that they may also depend on other factors. For example, in summer samplings, we found that herbicides selected small-sized early flowering species as found by Bopp et al. (2022) in three other wine regions of France, while other studies found that species in sprayed plots were rather high-sized (Guerra et al., 2021; MacLaren et al., 2019) and late flowering (Guerra et al., 2021). This could also be explained by the existence of several viable strategies in sprayed vineyards, a pure ruderal strategy or a combined competitive-ruderal strategy, which implies partly different trait values. Finally, both Guerra et al. (2021) and Hall et al. (2020) highlighted that mowing selects hemicryptophytes, the former with a stress-tolerant strategy, the latter with a competitive strategy. Our results partly reconcile these two studies since both hemicryptophytes with a C and CS strategy were selected by mowing, showing that again several strategies are viable. Actually, mowing has been shown to select for both traits related to competitive strategy as high stature (Bopp et al., 2022; Kazakou et al., 2016; Mainardis et al., 2020), but also trait values compatible with both C and S strategies such as high seed mass (Bopp et al., 2022; MacLaren et al., 2019) and low SLA values (Bopp et al., 2022; Guerra et al., 2021; Hall et al., 2020; Kazakou et al., 2016; Mainardis et al., 2020). In our study, there was a further separation between C- and S-strategists along a soil resource gradient that had a stronger structuring effect than fertilisation practices. However, the trait values selected on the fertile side of this gradient (high size and high seed mass) were consistent with the effects of irrigation found by Guerra et al. (2021).

5 | CONCLUSIONS

This study is one of the first to confirm that weed vegetation can be summarised by specific trait values and consistent strategies along two orthogonal gradients of disturbance and resource availability in relation to management practices and soil characteristics. Life forms, flowering phenology and SLA were mostly associated with the level of disturbance while plant height and seed mass were more related to competition-related mechanisms associated with soil fertility. Based on knowledge of the soil characteristics, it becomes possible to predict which type of weeds (major traits and CSR strategy) will occur according to the combination of practices applied on the rows and inter-rows.

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REFERENCES

Armengot, L., Blanco-Moreno, J., Bàrberi, P., Bocci, G., Carlesi, S., Aendekerk, R. et al. (2016) Tillage as a driver of change in weed communities: a functional perspective. *Agriculture, Ecosystems & Environment*, 222, 276–285.

Benjamini, Y. & Hochberg, Y. (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society: Series B (Methodological)*, 57, 289–300.

Boinot, S., Fried, G., Storkey, J., Metcalfe, H., Barkaoui, K., Lauri, P.É. et al. (2019) Alley cropping agroforestry systems: reservoirs for weeds or refugia for plant diversity? *Agriculture, Ecosystems & Environment*, 284, 106584.

Boisson, T. (2016) *Influence du paysage sur la flore adventice en viticulture* [MSc]. Grenoble, France: Université Grenoble Alpes.

Booth, B.D. & Swanton, C.J. (2002) Assembly theory applied to weed communities. *Weed Science*, 50, 2–13.

Bopp, M.-C., Kazakou, E., Metay, A. & Fried, G. (2022) Relative importance of region, seasonality and weed management practices effects on the functional structure of weed communities in French vineyards. *Agriculture, Ecosystems & Environment*, 330, 107892.

Colbach, N., Petit, S., Chauvel, B., Deytieux, V., Lechenet, M., Munier-Jolain, N. et al. (2020) The pitfalls of relating weeds, herbicide use, and crop yield: don't fall into the trap! A critical review. *Frontiers in Agronomy*, 2, 615470.

Cordeau, S., Wayman, S., Ketterings, Q.M., Pelzer, C.J., Sadeghpour, A. & Ryan, M.R. (2021) Long-term soil nutrient management affects taxonomic and functional weed community composition and structure. *Frontiers in Agronomy*, 3, 636179.

DeMalach, N., Ron, R. & Kadmon, R. (2019) Mechanisms of seed mass variation along resource gradients. *Ecology Letters*, 22, 181–189.

Dolédec, S., Chessel, D., ter Braak, C.J. & Champely, S. (1996) Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, 3, 143–166.

Dray, S., Choler, P., Dolédec, S., Peres-Neto, P.R., Thuiller, W., Pavoine, S. et al. (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95, 14–21.

Dray, S. & Dufour, A.-B. (2007) The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20.

Dray, S. & Legendre, P. (2008) Testing the species traits-environment relationships: the fourth-corner problem revisited. *Ecology*, 89, 3400–3412.

Duflot, R., Georges, R., Ernoult, A., Aviron, S. & Burel, F. (2014) Landscape heterogeneity as an ecological filter of species traits. *Acta Oecologica*, 56, 19–26.

Fried, G., Chauvel, B. & Reboud, X. (2009b) A functional analysis of large-scale temporal shifts from 1970 to 2000 in weed assemblages of sunflower crops in France. *Journal of Vegetation Science*, 20, 49–58.

Fried, G., Cordeau, S., Metay, A. & Kazakou, E. (2019) Relative importance of environmental factors and farming practices in shaping weed communities structure and composition in French vineyards. *Agriculture, Ecosystems & Environment*, 275, 1–13.

Fried, G., Kazakou, E. & Gaba, S. (2012) Trajectories of weed communities explained by traits associated with species' response to management practices. *Agriculture, Ecosystems & Environment*, 158, 147–155.

Fried, G., Petit, S., Dessaint, F. & Reboud, X. (2009a) Arable weed decline in Northern France: crop edges as refugia for weed conservation? *Biological Conservation*, 142, 238–243.

Gaba, S., Fried, G., Kazakou, E., Chauvel, B. & Navas, M.L. (2014) Agroecological weed control using a functional approach: a review of cropping systems diversity. *Agronomy for Sustainable Development*, 34, 103–119.

Gaba, S., Perronne, R., Fried, G., Gardarin, A., Bretagnolle, F., Biju-Duval, L. et al. (2017) Response and effect traits of arable weeds in agro-ecosystems: a review of current knowledge. *Weed Research*, 57, 123–147.

Gabriel, D., Thies, C. & Tscharntke, T. (2005) Local diversity of arable weeds increases with landscape complexity. *Perspectives in Plant Ecology, Evolution and Systematics*, 7, 85–93.

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

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, 250, 26–31.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111, 1169–1194.

Guerra, J.G., Cabello, F., Fernández-Quintanilla, C. & Dorado, J. (2021) A trait-based approach in a Mediterranean vineyard: effects of agricultural management on the functional structure of plant communities. *Agriculture, Ecosystems & Environment*, 316, 107465.

Gulden, R.H., Sikkema, P.H., Hamill, A.S., Tardif, F.J. & Swanton, C.J. (2010) Glyphosate-resistant cropping systems in Ontario: multivariate and nominal trait-based weed community structure. *Weed Science*, 58, 278–288.

Gunton, R.M., Petit, S. & Gaba, S. (2011) Functional traits relating arable weed communities to crop characteristics. *Journal of Vegetation Science*, 22, 541–550.

Hall, R.M., Penke, N., Kriechbaum, M., Kratschmer, S., Jung, V., Chollet, S. et al. (2020) Vegetation management intensity and landscape diversity alter plant species richness, functional traits and community composition across European vineyards. *Agricultural Systems*, 177, 102706.

Hodgson, J.G., Wilson, P.J., Hunt, R., Grime, J.P. & Thompson, K. (1999) Allocating C-S-R plant functional types: a soft approach to a hard problem. *Oikos*, 85, 282–294.

Honnay, O., Piessens, K., Van Landuyt, W., Hermy, M. & Gulinck, H. (2003) Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. *Landscape and Urban Planning*, 63, 241–250.

Julve P (1998) *Baseflor. Index botanique, écologique et chorologique de la flore de France*. Available at: http://perso.wanadoo.fr/philippe.julve/catminat.htm [accessed 12th May 2014].

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

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

MacLaren, C., Bennett, J. & Dehnen-Schmutz, K. (2019) Management practices influence the competitive potential of weed communities and their value to biodiversity in South African vineyards. *Weed Research*, 59, 93–106.

Maillet, J. (2006) Flore des vignobles: Biologie et écologie des mauvaises herbes. *Phytoma-La Défense des végétaux*, 590, 43–45.

Mainardis, M., Boscutti, F., Rubio Cebolla, M.M. & Pergher, G. (2020) Comparison between flaming, mowing and tillage weed control in the vineyard: effects on plant community, diversity and abundance. *PLoS One*, 15, e0238396.

May, F., Giladi, I., Ristow, M., Ziv, Y. & Jeltsch, F. (2013) Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. *Perspectives in Plant Ecology, Evolution and Systematics*, 15, 304–318.

Moog, D., Kahmen, S. & Poschlod, P. (2005) Application of CSR-and LHS-strategies for the distinction of differently managed grasslands. *Basic and Applied Ecology*, 6, 133–143.

Pierce, S., Negreiros, D., Cerabolini, B.E., Kattge, J., Díaz, S., Kleyer, M. et al. (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444–457.

Plaza, E.H., Navarrete, L. & González-Andújar, J.L. (2015) Intensity of soil disturbance shapes response trait diversity of weed communities: the long-term effects of different tillage systems. *Agriculture, Ecosystems & Environment*, 207, 101–108.

Ryan, M.R., Smith, R.G., Mirsky, S.B., Mortensen, D.A. & Seidel, R. (2010) Management filters and species traits: weed community assembly in long-term organic and conventional systems. *Weed Science*, 58, 265–277.

Santini, B.A., Hodgson, J.G., Thompson, K., Wilson, P.J., Band, S.R., Jones, G. et al. (2017) The triangular seed mass–leaf area relationship holds for annual plants and is determined by habitat productivity. *Functional Ecology*, 31, 1770–1779.

Simonovici, M. (2019) Enquête pratiques phytosanitaires en viticulture en 2016: nombre de traitements et indicateurs de fréquence de traitement. *Agreste Les Dossiers*, 2, 1–50.

Storkey, J. (2004) Modelling seedling growth rates of 18 temperate arable weed species as a function of the environment and plant traits. *Annals of Botany*, 93, 681–689.

Storkey, J., Moss, S.R. & Cussans, J.W. (2010) Using assembly theory to explain changes in a weed flora in response to agricultural intensification. *Weed Science*, 58, 39–46.

Team RC. (2020) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. https://www.R-project.org/

Trichard, A., Alignier, A., Chauvel, B. & Petit, S. (2013) Identification of weed community traits response to conservation agriculture. *Agriculture, Ecosystems and Environment*, 179, 179–186.

Wagner, H.H., Wildi, O. & Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology*, 15, 219–227.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, 33, 125–159.

Zanin, G., Otto, S., Riello, L. & Borin, M. (1997) Ecological interpretation of weed flora dynamics under different tillage systems. *Agriculture, Ecosystems and Environment*, 66, 177–188.

SUPPORTING INFORMATION

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