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RESEARCH ARTICLE

Drivers of species composition in arable-weed communities of the Austrian–Hungarian borderland region: What is the role of the country?

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Abstract

Questions: Due to their high ecological and agronomical variability, borderland regions offer an excellent opportunity to study assembly patterns. In this study we compared the influence of various factors on summer annual weed communities consisting of both native and introduced species.

Location: The borderland region of Austria and Hungary.

Methods: We assessed the abundance of weed species in 300 fields of six summer annual crops, and collected information on 26 background variables for each plot. We applied redundancy analysis (RDA) to estimate multivariate species responses and variation partitioning to compare the relative importance of three groups of variables (environmental variables, management variables, and country as a singleton group), and we also checked for statistical association between country and the predictors of the other two groups.

Results: The full RDA model explained 22.02% of the variance in weed species composition. Variation partitioning showed that environment and management had similarly high (~8%) influence on weeds, while country had a modest yet substantial (~1%) effect, and there was relatively little overlap between the variance attributable to the three groups. Comparing the individual variables, country ranked third (after preceding crop, and actual crop). The effects of 15 further variables were also significant, including seven management, and seven environmental variables, as well as the location of the sampling plots within the fields. Comparisons between the countries showed that farming type, preceding crops, tillage system, tillage depth and field size were significantly different between the countries.

Conclusions: Country exhibited a small but significant influence on weed community composition, which could not be explained with easily accessible management and environmental variables. This suggests that the distinct historical agronomical background of the two countries, possibly involving some legacies of the former Iron Curtain period, still has an impact on the weed species composition of arable fields.

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KEYWORDS
agriculture, annual crops, arable weeds, climate, country effect, ecological legacy, Iron Curtain, variance partitioning, weed survey, weed vegetation

1 | INTRODUCTION

In many parts of the world arable-weed communities create 'melting pots' for native and introduced species of diverse ecological and biogeographic backgrounds (Lososová et al., 2008; Bourgeois et al., 2019). Weed vegetation in arable fields is influenced by numerous environmental and management factors, and there have been many previous studies that evaluated and ranked their impacts on species composition in country scale (Fried et al., 2008; Pinke et al., 2012) and larger regional scale studies (Lososová et al., 2004; Šilc et al., 2009). The relative importance of environment vs human management factors was highly dependent on the explicit gradient lengths in the studies involved (Cimalová & Lososová, 2009; Pinke et al., 2016). New collections of data, such as the European Weed Vegetation Database (Küzmič et al., 2020), the Arable Weeds and Management in Europe (AWME) database (Bürger et al., 2020) and the AgriWeedClim database (Glaser et al., 2022), gave a recent impulse to re-establish such studies even at a Europe-wide scale. These new data sets create new opportunities for the detection of macro-ecological and biogeographical patterns and processes in weed communities (Bürger et al., 2022; Metcalfe et al., 2023). However, large-scale analyses can be efficiently complemented with local studies focussing on relevant areas of interest.

Due to the steep gradients and sudden changes in management factors, historical borderlands can be exciting areas for vegetation science to study both past (Rybníček & Rybníčková, 2008) and present (Poulos & Camp, 2010) natural vegetation types. Historical borderlands separating sharply distinct socio-economic zones, for example geo-political blocs, can be particularly interesting (Bičík et al., 2010). In such cases the long-standing separation can cause substantial persistent differences in many socio-economic factors (e.g., land-use practices, ownership structures), with cascading ecological implications (e.g., disturbance regimes) (Pinke et al., 2019). Consequently, borderlands are promising sites for intensive vegetation sampling, offering complex and profound insights into the impacts of heterogeneity in socio-ecological factors on vegetation, particularly on anthropogenic vegetation.

In this paper, we investigate the influence of a broad range of environmental and socio-economic factors (i.e., agricultural management) on the summer arable-weed communities of arable-crop fields in the former Iron Curtain borderland separating Austria and Hungary in Eastern Europe. In Austria this region is one of the most intensive agricultural regions of the country, which is sometimes considered as the main entry point for alien plants into the country (Follak et al., 2017). Similarly, Western Hungary is also often considered as an arable-weed hotspot in Hungary, in particular for species associated with relatively high precipitation (Pinke et al., 2016, 2018). A recent study along the Austrian–Hungarian border identified country-specific patterns in the infestation of several summer arable crops by the invasive weed *Ambrosia artemisiifolia*, which could be attributed to historical effects of the Iron Curtain and the consequent differences in management regimes (Pinke et al., 2019). In this study, we sample the same study area following a similar study design, but extending the analysis to the entire weed communitys. We seek answers to the following two broad questions:

1. How much do management and the environment influence the species composition of summer annual arable-weed vegetation in this region? Which variables have a quantifiable effect on species composition, and which weed species can be associated with these variables?
2. How does the country relate to these groups of variables? How much of the influence of management and environmental variables can also be explained by the country, and are there residual country effects not covered by either group of variables? Which weed species can be associated with the two countries? And what are the significant differences in terms of management and environmental variables?

2 | METHODS

2.1 | Study area

Our study area was a strip of land along the national borderline between Austria and Hungary, extending approximately 30 km into each country on both sides. This gives an irregularly curved zigzag-shaped area that is stretching approx. 150 km N–S and approx. 100 km E–W (Figure 1). The northern section of this strip lies in a lowland area of the Pannonian Basin, which extends into the foothills of the Eastern Alps towards the south, with decreasing altitudes from West (Austria) to East (Hungary), which leads to considerable yet strongly correlated gradients in several environmental variables (e.g., altitude, temperature, precipitation). Furthermore, the two countries, separated by the Iron Curtain, followed highly different socio-economic trajectories in the last century, which may still cause differences in the management practices. Table 1 presents more details about the ranges of the geographic and environmental parameters in the study area.

2.2 | Data collection

First, we searched for farmers in the study area who permitted us to access to their fields and were willing to be interviewed about management factors. We focussed on fields with six major regional

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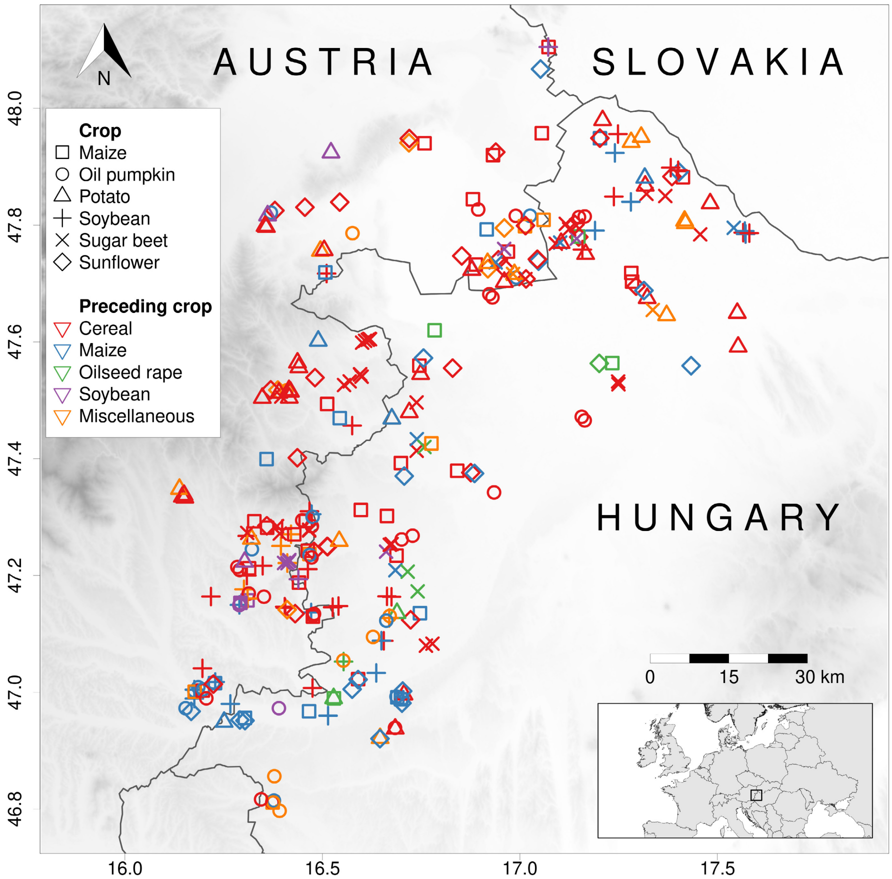

FIGURE 1 Map showing the spatial distribution, the *crop* types, and the *previous crop* types of the 300 fields surveyed along the Austrian–Hungarian border. Crop is indicated by the shape and preceding crop by the colour.

crops: sunflower (*Helianthus annuus*), soybean (*Glycine max*), maize (*Zea mays*), oil pumpkin (*Cucurbita pepo*), sugar beet (*Beta vulgaris*), and potato (*Solanum tuberosum*). Altogether, 300 fields were sampled (25 fields of each crop per country). Weed data were recorded between the years 2015 and 2022 at the seasonal peak of summer annual weed vegetation from mid-July until early September each year. Sampling was done in four rectangular plots of 5 m × 10 m within each field. One plot was located at the edge of a field (inside the outermost seed drill line) and the other three plots were located inside the fields at different distances (between 10 and 200 m) from the edge. Otherwise, the plots were placed randomly in the fields. In each plot the percentage ground cover of each weed species and the crop was estimated visually. A soil sample of 1000 cm^3 from the top 10-cm layer was also collected from the centre of each field, and was analysed in the laboratories of Synlab Hungary Ltd and BETA Research Institute. Taxonomic nomenclature followed Király (2009), while the origin and conservation status of each species were extracted from Sonkoly et al. (2023).

Information on management was obtained directly from the farmers in brief targeted interviews. In order to avoid rare levels of categorical variables, infrequent types of preceding crops (occurring less than 10 times) were merged in a single category ('miscellaneous' crops). Similarly, due to the high diversity of herbicides (59 active ingredients were applied in the 300 fields), we only considered the number of active ingredients as a proxy of chemical weed control in our analysis. Climatic variables (mean annual temperature and annual precipitation sum) were obtained from the WorldClim 2.0 database (Fick & Hijmans, 2017). Two additional variables were also recorded during the surveys: the country of the observations, and the position of the sampling plot in the field (plot location: field margin vs field core). Altogether we compiled a list of 26 predictor variables for the analysis, most of which can be classified as either environmental (11 variables) or management variables (13). Country and plot location were considered to belong to neither of these groups (Table 1).

2.3 | Data analysis

We first created a full RDA model with all of the predictors identified above. Cover values of the weed species were averaged across all three plots from each field core to ascertain the average community composition of the inner part of the individual fields. Data from field edges were regarded separately. Cover values were subjected to Hellinger transformation (Borcard et al., 2011), and were examined in a redundancy analysis (RDA) together with the management and environmental data. Only species with more than 10 occurrences were included in the analyses. We applied variation partitioning on this RDA model, dividing the adjusted R^2 (R^2_{adj}) values between the two main groups of explanatory variables and country as a third 'group' in order to compare the relative importance of these three groups (Peres-Neto et al., 2006; Borcard et al., 2011).

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TABLE 1 The list of variables applied in the study to characterize the weed survey locations, together with their units, ranges, and mean values (for continuous variables), or the set of eligible values (for categorical variables).

Variable (unit)	Range/values	Mean values	
		Austria	Hungary
Environmental variables			
Altitude (m)[a]	111–429	243.3	178.1
Annual total *precipitation* (mm)[a]	535–766	662.5	623.8
Annual mean *temperature* (°C)[a]	9.04–10.38	9.7	9.9
Soil pH (in KCl, dimensionless)	3.73–7.83	6.3	6.2
Soil texture (KA)	25–66	40.9	40.7
Soil humus content (m·m%$^{-1}$)	0.7–16.2	2.4	2.2
Soil Ca content ($CaCO_3$, m·m%$^{-1}$)	0.1–35.1	3.1	5.7
Soil P content (P_2O_5, mg·kg^{-1})[b]	20–2920	246.5	287.2
Soil K content (K_2O, mg·kg^{-1})	65.7–1050	287.2	272.1
Soil Na content (Na, mg·kg^{-1})	9–235.9	47.8	53.9
Soil Mg content (Mg, mg·kg^{-1})	47.4–883	286.3	281.3
Management variables			
Crop type	Maize, oil pumpkin, potato, soybean, sugar beet, sunflower	–	–
Crop cover (%)	0–100	75.2	78.1
Preceding crop type	Cereal, maize, oilseed rape, soybean, miscellaneous	–	–
Farming type	Conventional, organic	–	–
Field size (ha)	0.17–80	4.5	12.6
Primary *tillage depth* (cm)[b]	3–50	23.5	30.7
Tillage system[b]	No-tillage, ploughing	–	–
Organic manure (t·ha^{-1})[b]	0–100	4.1	6.2
N fertiliser (N, kg·ha^{-1})[b]	0–300	46.3	66.6
P fertiliser (P_2O_5, kg·ha^{-1})	0–260	30	47.1
K fertiliser (K_2O, kg·ha^{-1})	0–300	36.6	64
Mechanical weed control (number of applications)	0–9	1.5	1.2
Chemical weed control (number of active ingredients)	0–10	1.6	3.2
Other variables			
Country	Austria, Hungary	–	–
Plot location	Edge, core	–	–

[a]Altitude, precipitation, and temperature were included into the *reduced model* through their first principal component due to multicollinearity.

[b]Variables excluded from the *reduced model* during the backward selection process.

We then applied a two-step procedure to identify a minimal adequate reduced model with a parsimonious set of independent predictors. First, we assessed the multicollinearity of the variables (potential model terms) by calculating generalised variance inflation factors (GVIF). Altitude, mean annual precipitation, and mean annual temperature had high GVIF due to strong pairwise correlations among these variables (altitude–temperature, −0.96; altitude–precipitation, 0.86; temperature–precipitation, −0.91; Appendix S1). Accordingly, we replaced altitude, precipitation, and temperature with their first principal component, which we call 'topoclimate' henceforward. This first principal component explained 94% of the total variation of the three variables. Positive topoclimate values are associated with high altitude, high precipitation and low temperature (Appendix S1). As the rest of the variables showed only slight collinearity (max[GVIF] = 1.881), we then proceeded with a stepwise backward selection using a $p < 0.01$ threshold for type-I error, which led to our reduced RDA model with 19 terms.

As the next step of the multivariate analysis, we estimated the gross and net effects of each explanatory variable in the reduced

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model. Following Lososová et al. (2004), gross effects were defined as the variation explained in a univariate RDA model having just the focal variable as the only predictor, whereas net effects were quantified as the variance explained by the focal variable in a partial RDA model (pRDA), having all other variables as co-variates. Based on the R^2_{adj}-values of the net effects, we also established a common rank of 'importance' among the explanatory variables. To explore the responses of the different weed species, for each variable we identified those 10 species that represented the highest explained variation in the constrained axis/axes ('strongly associated' species), and for crop, and preceding crop we also plotted ordinations along the first two RDA axes.

To zoom in on the effect of the country for the individual crop species we first performed a global test of significance for the 'crop:country' interaction term partialling all other variables out from the model. This was followed by performing a pRDA for the effect of *country* for each *crop* species separately, identifying this way the 10 most 'country-specific' weeds for each of the six crops studied.

To get a better insight into the background of the 'cross-border' weed community patterns detected, we also assessed the 'direct associations' between country and the other (environmental, management) predictors. To achieve this for continuous variables we compared their means in the two countries (*t*-tests using the Welch approximation, preceded by log transformation for apparently right-skewed variables), and for categorical variables chi-squared tests of homogeneity were performed.

Finally, we also performed an indirect gradient analysis to establish that there are no other dominant gradients in our data set. The indirect gradient analysis in the unconstrained ordination (PCA) showed that the first axis explained 12.75%, while the first RDA axis explained only 7.2%. However, if the background variables of the first RDA axis were projected on the unconstrained ordination axis, they are changing along it, but not linearly (Appendix S1). These suggest that no other important variables are missing.

The entire statistical analysis was conducted in the R environment (R Development Core Team, version 3.2.2) using the *vegan* package (vegan 2.3e1) (Oksanen et al., 2022).

3 | RESULTS

Altogether, 217 weed species were recorded, but only 78 species had more than 10 occurrences (Appendix S1). The full RDA model (comprising 24 explanatory variables) explained 22.02% of the variance. The variation partitioning revealed that both management and environmental variables explain approx. 8% of the variance in weed species, with environment being slightly more influential than management. Country alone could explain approx. 1% of the total variance, most of which was unique to this variable (not shared with either of the two other groups, Figure 2). All overlaps between the variance components were relatively modest: for any pair of groups the shared variance was less than 16% of the variance explained by the less influential group.

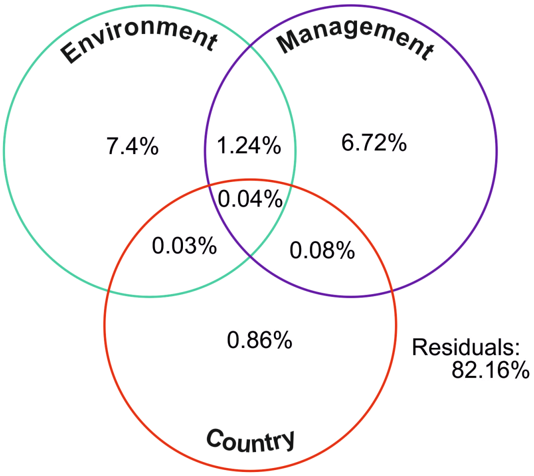

FIGURE 2 Percentage contributions of groups of explanatory variables to the variation in weed species composition, identified by partitioning of the adjusted R^2: environmental vs management variables vs country (plot location is included in the residuals here).

Five predictors (soil P, tillage system, tillage depth, organic manure, and N fertiliser) were dropped during the backward selection process. Accordingly, the reduced RDA model contained 19 predictors, including nine management variables (preceding crop, crop, crop cover, farming type, mechanical weed control, fertiliser P, fertiliser K, number of herbicides, and field size), eight environmental variables (topoclimate, soil pH, soil Mg, soil Ca, soil K, soil texture, humus, and soil Na), as well as country, and sampling plot location. This reduced model still explained 21.19% of the total variation in species data. With the exception of soil Na, all variables were found to be significant in the pRDA models, and a common order of importance was established, where preceding crop ranked first, crop occupied the second, and country the third position (Table 2).

As the effect of the crop:country interaction term was significant in the respective pRDA model, we also looked at the gross and net effects of country for each individual crop species. The net effect of country was still significant in all of the studied cultures, except for soybean (Table 3).

In the reduced RDA ordination, the first axis can be most related to the explanatory variables soil pH, K, Ca, Na and humus content, mechanical weed control, as well as topoclimate. Furthermore, the two root crops (sugar beet and potato) are also separated from the other crops along the first axis. Samples with higher topoclimate values (more humid and cool regions at higher altitudes) are typically characterised by more acidic soils poor in potassium and calcium (Figure 3a, b). Displaying the weed species to the same ordination reveals that such sites exhibit higher abundances of *Setaria pumila*, *Chenopodium polyspermum*, *Persicaria lapathifolia*, *Equisetum arvense*, and *Calystegia sepium*. In contrast, sites in the drier and warmer regions at lower altitudes, with more basic and K-rich soils show higher abundance of *Datura stramonium*, *Chenopodium hybridum*, and *Mercurialis annua*, and low axis-1 values.

The second axis is mostly correlated with country, plot location and crop cover. Negative values along the second axis are mainly

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TABLE 2 Gross and net effects of the explanatory variables on the weed species composition identified using (partial) RDA analyses.

Factors	df	Gross effect: Explained variation (%)	Gross effect: R^2_{adj}	Net effect: Explained variation (%)	Net effect: R^2_{adj}	F	p-value
Preceding crop	4	1.800	0.0114	1.321	0.8006	2.4017	0.001
Crop	5	4.574	0.0377	3.772	0.0320	5.4855	0.001
Country	1	1.395	0.0123	1.256	0.0123	9.1324	0.001
Topoclimate[a]	1	5.126	0.0497	1.008	0.0091	7.3317	0.001
Crop cover	1	1.267	0.0110	0.838	0.0073	6.0910	0.001
Plot location	1	1.088	0.0092	0.709	0.0060	5.1532	0.001
Soil pH	1	4.858	0.0469	0.680	0.0057	4.9433	0.001
Soil Mg content	1	0.685	0.0052	0.552	0.0043	4.0156	0.001
Soil Ca content	1	3.124	0.0296	0.523	0.0040	3.8009	0.001
Soil K content	1	2.695	0.0253	0.431	0.0031	3.1307	0.001
Farming type	1	1.059	0.0089	0.396	0.0027	2.8812	0.001
Mechanical weed control	1	1.211	0.0104	0.350	0.0022	2.5412	0.001
Soil texture	1	0.568	0.0040	0.343	0.0021	2.4943	0.001
Fertiliser P	1	0.932	0.0076	0.332	0.0020	2.4141	0.005
Fertiliser K	1	0.798	0.0063	0.315	0.0018	2.2874	0.007
Number of herbicides	1	0.655	0.0048	0.289	0.0016	2.1045	0.009
Field size	1	0.704	0.0053	0.289	0.0016	2.1022	0.006
Soil humus content	1	1.062	0.0089	0.258	0.0013	1.8764	0.014
Soil Na content	1	1.778	0.0161	0.225	0.0009	1.6322	0.055

[a]Altitude, precipitation, and temperature were replaced with their first principal component (see more in Appendix S1).

TABLE 3 Gross and net effects of the explanatory variable *crop* on the differences in weed species composition in the same crop type between the countries identified using (partial) RDA analyses.

Factors	*df*	Gross effect: Explained variation (%)	Gross effect: R^2_{adj}	Net effect: Explained variation (%)	Net effect: R^2_{adj}	F	p-value
Oil pumpkin	1	3.442	0.0246	2.796	0.0259	3.9903	0.001
Maize	1	2.314	0.0132	2.014	0.0160	2.7234	0.001
Sunflower	1	3.715	0.0273	1.518	0.0093	1.9843	0.006
Sugar beet	1	4.390	0.0341	1.382	0.0073	1.7298	0.033
Potato	1	4.668	0.0370	1.301	0.0070	1.7512	0.03
Soybean	1	2.706	0.0171	1.164	0.0045	1.4437	0.115

characteristic of field cores with high crop cover in Austria, without any clearly associating species. High axis-2 values, on the other hand, mainly refer to field edges with low crop cover in Hungary, generally with higher abundance of *Ambrosia artemisiifolia* (Figure 3c).

Based on the partial RDA models, we identified the 10 most associated weed species (the ones with the highest pRDA fit) for each variable, together with their specific responses. For the three most influential variables (crop, preceding crop, and country), we present these species in Figure 4 and Table 4, while for the other variables these species are listed in Appendix S1.

As crop and preceding crop are nominal variables, the association between them (the different crops) and the most related weed species can be best presented in ordinations (Figure 4). In the case of crop there were four significant RDA axes, while for preceding crop, two constrained axes were significant at the $\alpha = 0.05$ level. All six studied crop species exhibit fairly distinct positions in the ordination diagram (Figure 4a): the two tallest crops (maize and sunflower) are separated from the shorter crops (soybean, sugar beet, oil pumpkin and potato) along the first axis, while sunflower, soybean and sugar beet are separated from the others along the second axis (Figure 4a).

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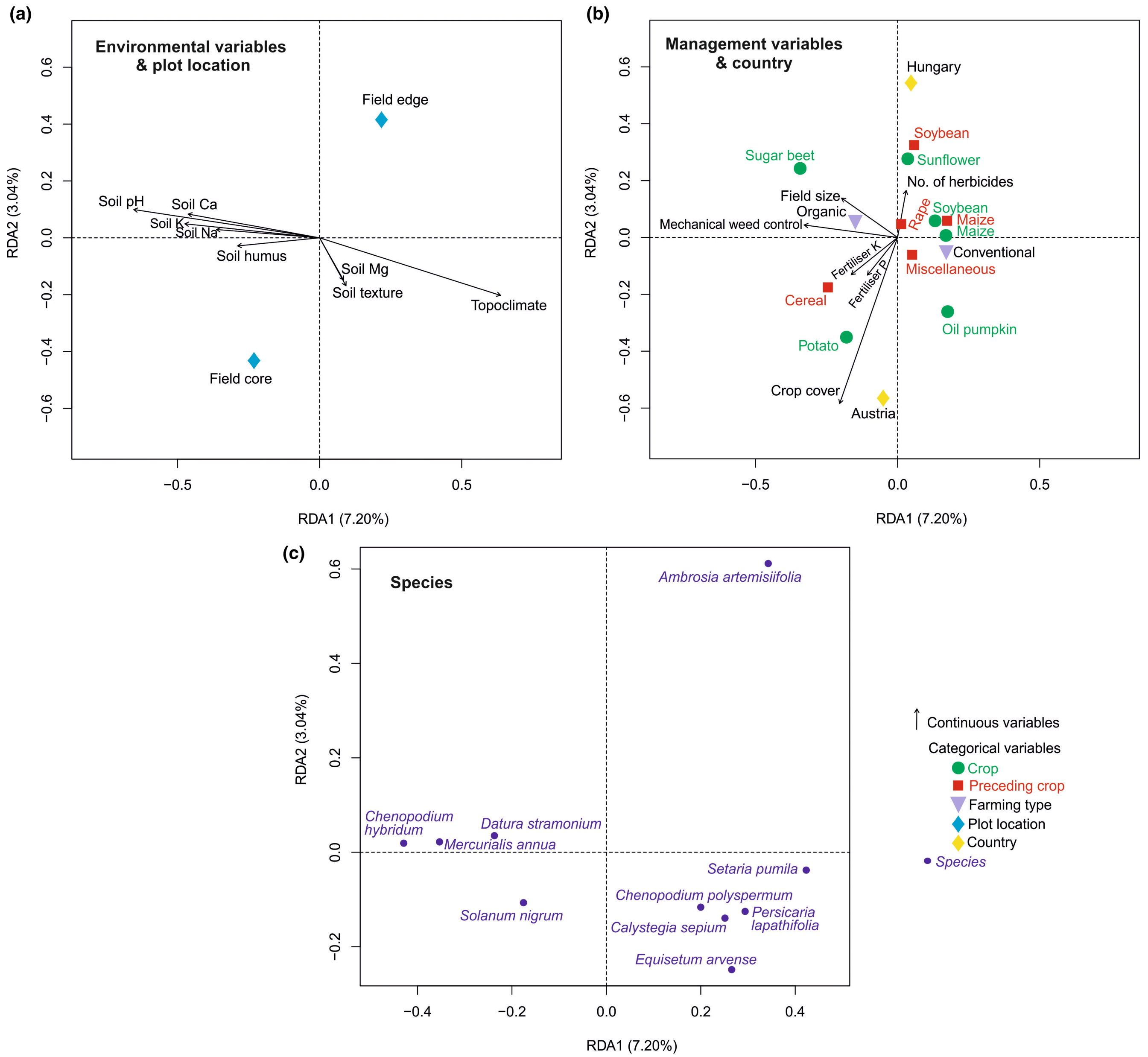

FIGURE 3 Ordination diagrams of the reduced redundancy analysis (RDA) model containing the (a) environmental variables and plot location, (b) management variables and country and (c) species. Only the ten species with the highest weights on the first two RDA axes are presented.

The most obvious preference can be detected by *Chenopodium album* towards the oil pumpkin fields along the first axis, while that of *Ambrosia artemisiifolia* can be traced towards soybean fields along the second axis. Other weed species are located very close to the centre of the ordination diagram (Figure 4a). On the ordination of preceding crops, typically autumn-sown crops (cereal and oilseed rape) are associated with one typical weed species (*Chenopodium album*), and they are separated along the first axis from spring-sown crops (maize and soybean) with *Ambrosia artemisiifolia* as their most characteristic weed (Figure 4b).

Among the weeds most associated with country, *Ambrosia artemisiifolia* and *Abutilon theophrasti* were more abundant in Hungary, while *Solanum nigrum* and *Portulaca oleracea* were more abundant in Austria (Table 4). The most country-associated weed, *Ambrosia artemisiifolia* was significantly more abundant in Hungarian fields for maize, pumpkin and potato. *Abutilon theophrasti*, on the other hand, showed a more complex pattern: in maize and pumpkin it was more abundant in Hungary, whereas in sugar beet fields, it was more associated with Austria (Table 4).

Appendix S1 also shows that *Ambrosia artemisiifolia* was negatively associated with crop cover and field size, while *Abutilon theophrasti* appeared to be susceptible to mechanical weed control, but was favoured by P fertiliser. Furthermore, *Chenopodium album* preferred Mg and humus-rich soils; while *Datura stramonium* clearly preferred the warm and arid end of the topoclimate spectrum, with base-rich soils, and sites with no mechanical weed control.

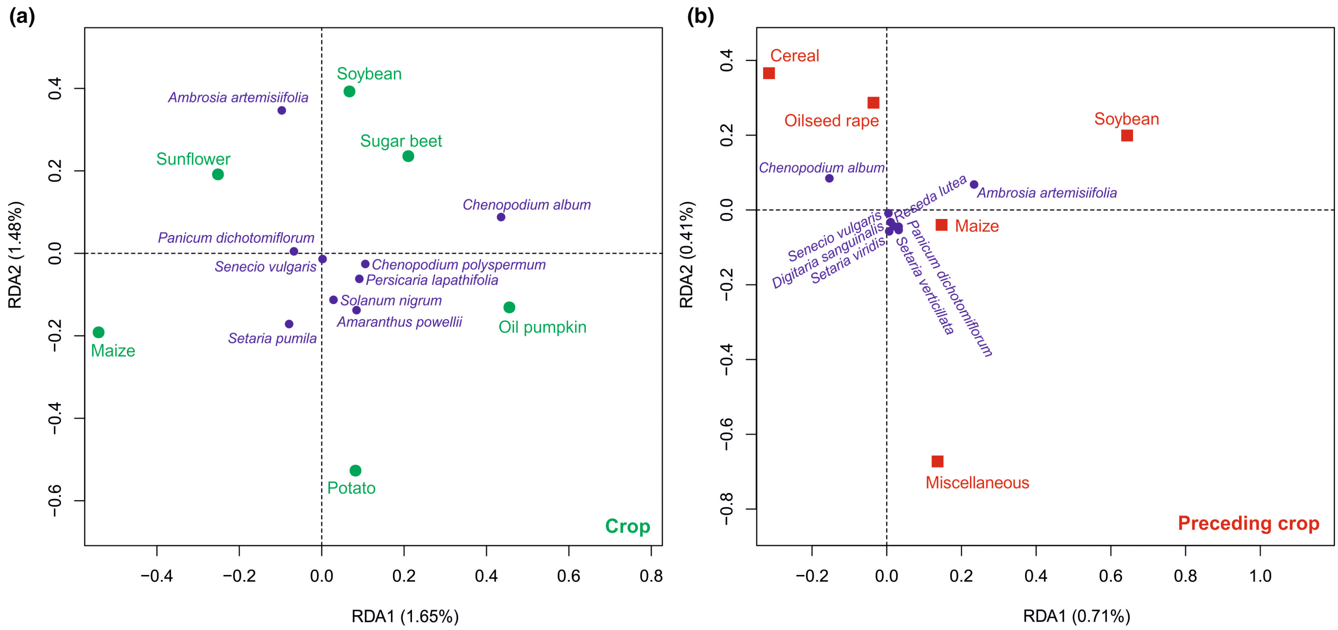

FIGURE 4 Ordination diagram of the partial redundancy analysis (RDA) model containing the explanatory variable (a) crop and (b) preceding crop. The ten species with the highest weight on the first two RDA axes are presented. Note that the first four (a) and the first two (b) axes are significant at $\alpha = 0.05$ level.

Although the variance shared between country and the other groups of variables was relatively small (Figure 2), we could still find several significant pairwise differences between the two countries both in management and environmental variables (Table 5, Figures 5 and 6). In line with the topoclimatic gradient discussed before, the mean altitude and precipitation was higher in the Austrian fields, while temperature, and soil Ca content were higher in Hungary. In terms of management, Austria could be characterised with significantly smaller field sizes, a higher proportion of fields managed both organically and in a no-tillage system, and a shallower average tillage depth. Furthermore, rape was a more frequent preceding crop in Hungary, while soybean was more frequent in Austria. The mean amount of all fertilisers and the number of herbicide ingredients were also significantly higher in Hungary.

4 | DISCUSSION

4.1 | Management variables

The two crop-related factors, the preceding and the actual crop species, were found to be the two most influential variables determining weed community composition in our study. Previous studies in France (Fried et al., 2008), Czechia (Cimalová & Lososová, 2009), Romania (Nagy et al., 2018) and Tajikistan (Nowak et al., 2015) also suggest that the crop species actually being cultivated is the most important factor determining the weed vegetation of arable fields. According to Fried et al. (2008), the dominant role of the crop in shaping weed communities is established through differences in sowing season (divergent sowing dates induce the development of distinct weed communities) and other crop-specific management variables (e.g., specific herbicide or fertilisation regimes). Gunton et al. (2011) also found that crop sowing time was among the most important predictors for weed community composition; and the importance of sowing season was also remarkably noticeable in poppy fields, showing a clear distinction between the weed flora of autumn-sown food poppy and spring-sown alkaloid poppy crops (Pinke et al., 2011). Recent studies in Germany and France also revealed that crop type and sowing date appeared as key factors in structuring weed communities (Seifert et al., 2015; Mahaut et al., 2019; Adeux et al., 2022). Furthermore, Metcalfe et al. (2023: p. 9) demonstrated that 'there are more similarities between weed communities of a given crop in different European regions than between weed communities of two different crops within the same region', which suggests that weed communities are principally governed by crop type, even at a continental scale.

Cimalová and Lososová (2009) distinguished cereal and root crops, explaining their different impacts on weed communities with differences in their sowing date and the length, duration, character, and intensity of the subsequent disturbances. According to Nowak et al. (2015), the strong influence of crop type is related to the different farming practices in roots and cereals. In our study, all of the six crop plants were sown in spring, and consequently, we only expected a clear separation between the two root crops (potato and sugar beet) and the other four crops. One of our ordination diagrams indicates a similar distinction (Figure 3b). Nonetheless, our diagrams also suggest some segregation across another key characteristic of the crops: their stature. Taller crops (maize and sunflower) were separated from typically shorter crops (potato, oil pumpkin, sugar beet, and soybean; Figure 4a). This can be most likely attributed

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TABLE 4 Names, fit, and score values of species giving the highest fit along the first constrained axis in the partial redundancy analysis (RDA) models of the crop variable in the same crop type between the countries.

	Axis 1 score	Fit		Axis 1 score	Fit
All crops (+ Austria, − Hungary)			Oil pumpkin (+ Austria, − Hungary)		
Ambrosia artemisiifolia	−0.3396	0.0548	*Abutilon theophrasti*	−0.1427	0.099
Abutilon theophrasti	−0.1614	0.0520	*Panicum miliaceum*	−0.0867	0.0986
Solanum nigrum	0.0903	0.0298	*Ambrosia artemisiifolia*	−0.2789	0.0903
Portulaca oleracea	0.0888	0.0255	*Persicaria amphibia*	−0.0269	0.0874
Equisetum arvense	0.1289	0.0252	*Capsella bursa-pastoris*	−0.0596	0.0734
Galinsoga parviflora	−0.0531	0.0247	*Equisetum arvense*	0.1981	0.0704
Setaria verticillata	0.0547	0.0233	*Lolium perenne*	0.0210	0.0634
Capsella bursa-pastoris	−0.0533	0.0192	*Lathyrus tuberosus*	0.0393	0.0482
Alopecurus myosuroides	−0.0235	0.0190	*Mercurialis annua*	0.0729	0.0455
Brassica napus	−0.0555	0.0180	*Oxalis stricta*	−0.0199	0.0418
Potato (+ Austria, − Hungary)			Sunflower (+ Austria, − Hungary)		
Brassica napus	−0.1426	0.162	*Alopecurus myosuroides*	−0.0798	0.1587
Alopecurus myosuroides	−0.0172	0.1313	*Panicum miliaceum*	−0.1664	0.0918
Stachys annua	0.0290	0.0507	*Viola arvensis*	−0.1011	0.0760
Helianthus annuus	0.0297	0.0485	*Reseda lutea*	−0.0408	0.0617
Avena fatua	−0.0420	0.0450	*Rubus caesius*	−0.0457	0.0509
Setaria pumila	0.1479	0.0408	*Geranium pusillum*	−0.0021	0.0474
Beta vulgaris	−0.0035	0.0397	*Solanum nigrum*	0.0550	0.0431
Matricaria chamomilla	−0.0144	0.0385	*Amaranthus retroflexus*	0.0809	0.0400
Sinapis arvensis	0.0133	0.0333	*Setaria verticillata*	0.0540	0.0350
Ambrosia artemisiifolia	−0.1104	0.0292	*Atriplex patula*	0.0164	0.0282
Sugarbeet (+ Austria, − Hungary)			Maize (+ Austria, − Hungary)		
Amaranthus blitoides	−0.0524	0.0763	*Ambrosia artemisiifolia*	−0.2728	0.0893
Lathyrus tuberosus	−0.0396	0.0721	*Abutilon theophrasti*	−0.1462	0.0892
Equisetum arvense	−0.0320	0.0677	*Lactuca serriola*	−0.0076	0.0869
Polygonum aviculare	−0.1103	0.0414	*Mercurialis annua*	0.1160	0.0477
Persicaria amphibia	−0.0146	0.0399	*Solanum nigrum*	0.0384	0.0470
Amaranthus retroflexus	−0.1390	0.0362	*Robinia pseudoacacia*	0.0316	0.0462
Abutilon theophrasti	0.1156	0.0360	*Silene alba*	−0.0070	0.0411
Stachys annua	−0.0231	0.0327	*Equisetum arvense*	0.1050	0.0380
Carex hirta	0.0061	0.0310	*Rubus caesius*	−0.0378	0.0273
Convolvulus arvensis	0.0964	0.0303	*Portulaca oleracea*	0.0759	0.0246

to the different light conditions of these crops as weed habitats: the taller the crop canopy is, the more intensively it can suppress weed growth by overshading (Lehnhoff et al., 2013; Jha et al., 2017; Rasmussen et al., 2021). Weed-suppressive crop species are generally able to increase their plant height when they are shaded by competition. Such crops typically have a wider and taller stature with a large specific leaf area (Colbach et al., 2019) that allows them to form a dense canopy maximising competitive avoidance/competitive confrontation (Novoplansky, 2009; Botta-Dukát, 2021). Anyway, a dense weed-suppressive crop canopy is not necessarily the sole consequence of crop type (and concomitant factors like crop height), but it can also be influenced by several other cultural practices, including seeding rate, plant density, spatial uniformity, and fertiliser use (Weiner, 2023). This study also underlines the

TABLE 5 Chi-squared test for homogeneity of the categorical and count variables between the countries.

Variables	Chi-squared (χ^2)	*df*	*p*-value
Farming type	27.83	1	<0.001
Preceding crop	19.57	4	<0.001
Tillage system	9.74	1	0.002
No. of herbicides	47.93	9	<0.001
No. of herbicides >2, in conventional farming	3.30	1	0.069
Mechanical weed control	9.36	9	0.404

importance of crop cover on weed species composition, similarly to experiences in Hungarian pumpkin (Pinke et al., 2018) and phacelia (Pinke et al., 2022) fields.

In this study, the preceding crop turned out to be the most important variable. Similarly to the case of the 'actual' crop, the effects of the preceding crop can also be 'mediated' through its sowing time: autumn-sown preceding crops (which are predominantly winter cereals and oilseed rape in this region) were clearly separated from spring-sown preceding crops (maize and soybean) (Figure 4b). This suggests that the crop species, and particularly its sowing season, has a long-lasting impact on weed species composition that can be traced even in the weed communities of the subsequently grown crops. In addition, the different harvest period of the autumn- or spring-sown previous crops can also influence the following weed emergence patterns (Colbach et al., 2005). Preceding crop was found to be an important driver also in the weed vegetation of Hungarian sunflower (Pinke et al., 2013), oil pumpkin (Pinke et al., 2018) and phacelia (Pinke et al., 2022) fields, apparently for sowing-time-related reasons, as well. The impact of the preceding crop was also relevant in oilseed rape and maize in Germany (Hanzlik & Gerowitt, 2011; de Mol et al., 2015), in arable fields in France (Fried et al., 2008), as well as in organic spring cereals in northern Europe (Hofmeijer et al., 2021).

We documented significant effects of several further cultural variables, including fertiliser P and K, farming type, and field size, all of which had a significant effect on the weed species composition in our analyses (Table 2). This is in accordance with the findings of other studies in Hungary and Europe. Fertilisers also had an impact on the weed flora of Hungarian soybean (Pinke et al., 2016) and oil pumpkin (Pinke et al., 2018) fields, because several weed species are also highly responsive to them, and their application can affect the overall crop–weed competition as well (Little et al., 2021). Furthermore, remarkable differences in the weed flora (Henckel et al., 2015) and weed seed bank (Rotchés-Ribalta et al., 2020) were documented in studies comparing organic and conventional farming; and the size of the fields also appears to impact their weed diversity (Petit et al., 2013; Tscharntke et al., 2021).

In our study, both of the recorded weed management variables (mechanical and chemical weed control) appeared to be relevant (Table 2). While we could not include each herbicide separately into our analysis, even the number of active ingredients applied was an important predictor for weed species composition. We performed a similar simplification for the mechanical treatments, applying just the number of different treatment operations (including cultivating tillage and manual weed control, e.g., hand hoeing, pulling, and weed-cutting operations) as our indicator, which was still found to be significant. The efficiency of such treatments has already been demonstrated in the same region where they could reduce the abundance of pernicious weeds in oil pumpkin fields (Pinke et al., 2018), but they were not significant either in poppy (Pinke et al., 2011) or sunflower (Pinke et al., 2013) or soybean fields (Pinke et al., 2016). The fact that in this study we detected a significant influence of mechanical treatments on weed communities might partly be due to the greater technical expertise of Austrian farmers in non-chemical weed management. This could also explain the lower abundances of *Ambrosia artemisiifolia* in organically farmed fields in Austria compared to those in Hungary (Pinke et al., 2019).

4.2 | Environmental variables and plot location

In our study, the fourth most important variable affecting weed flora (Table 2) was topoclimate, a synthetic variable combining the highly collinear effects of altitude, mean annual temperature, and annual total precipitation in our sample. This combination cannot only be justified by the strong correlations between the variables but also for ecological reasons, as the plant species are not affected directly by altitude, only through related climatic variables (Slavich et al., 2014; Rita et al., 2023). A complex gradient of increasing altitude and precipitation and decreasing temperature was found to be a major driver for arable-weed composition in central (Lososová et al., 2004) and southern (Pál et al., 2013) Europe, as well as Tajikistan (Nowak et al., 2015). Similar findings were also reported in crop-specific studies throughout Europe, including soybean (Pinke et al., 2016), oil pumpkin (Pinke et al., 2018), rape (Hanzlik & Gerowitt, 2011) and maize (de Mol et al., 2015), as well as in winter-arable crops (Fanfarillo et al., 2020); where precipitation and/or temperature were also relevant.

Among the soil parameters soil pH appeared to be the most important predictor (Table 2). As known in European biogeography, the continental 'distribution' of pH values in Europe largely follows the gradients of annual rainfall (Lu et al., 2023). This results in remarkable patterns in weed communities, with species linked to basic soils in drier areas and others characteristic of acidic soils in areas

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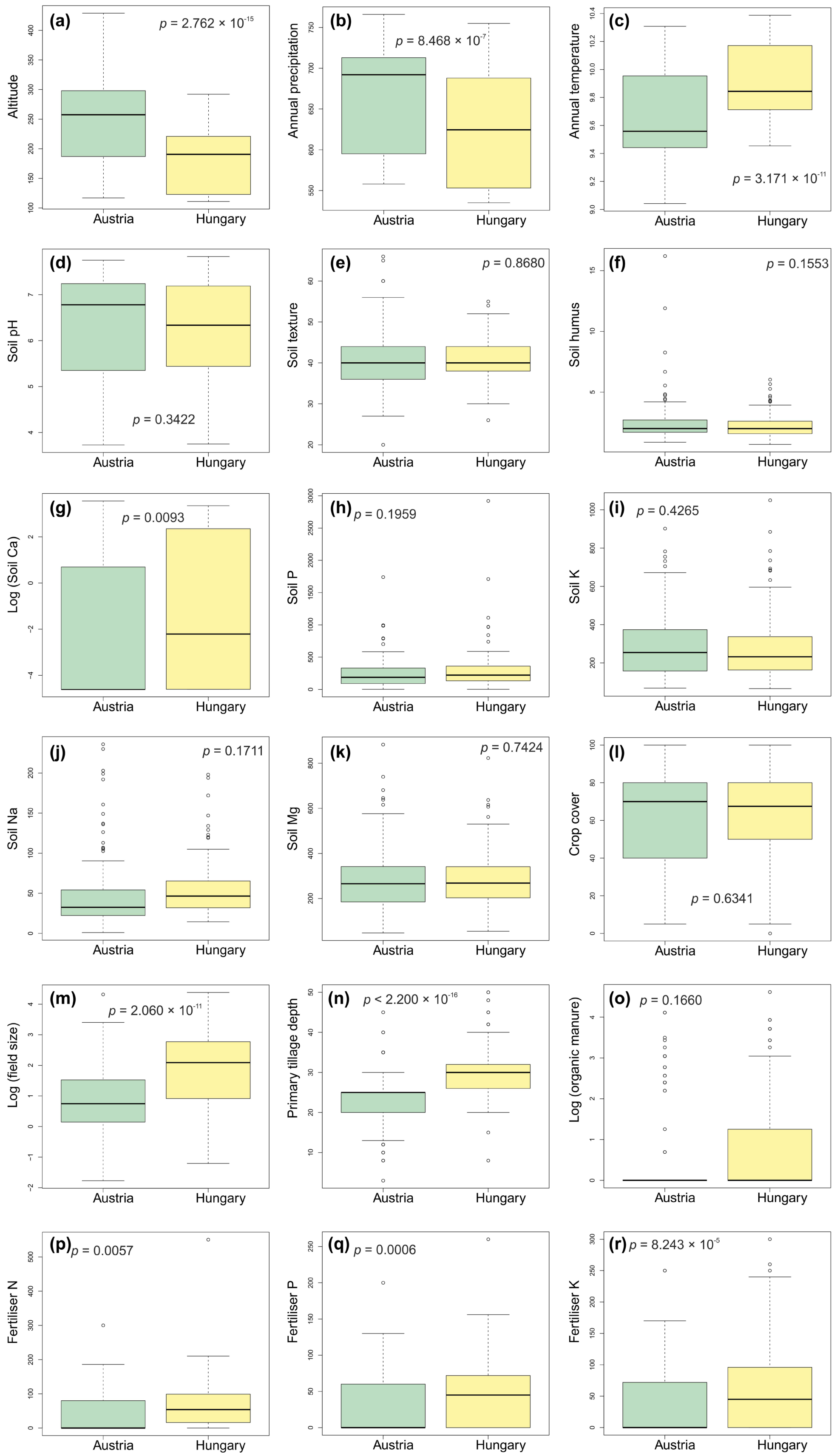

FIGURE 5 Comparisons across countries of the continuous predictor variables using *t*-tests with Welch approximation. (a) Altitude; (b) precipitation; (c) temperature; (d) soil pH; (e) soil texture; (f) soil humus; (g) soil Ca; (h) soil P; (i) soil K; (j) soil Na; (k) soil Mg; (l) crop cover; (m) field size; (n) tillage depth; (o) manure; (p) fertiliser N; (q) fertiliser P; (r) fertiliser K.

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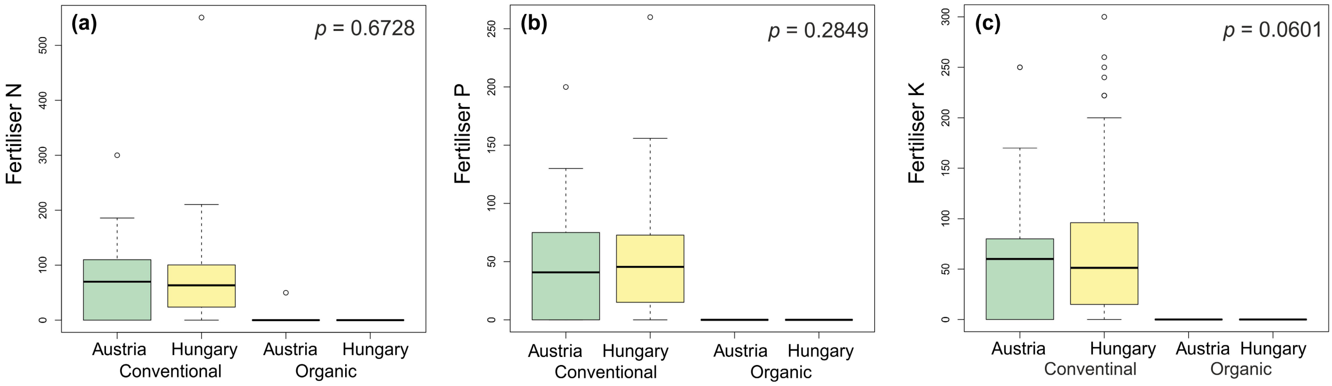

FIGURE 6 Comparisons of (a) N fertiliser, (b) P fertiliser and (c) K fertiliser use between organic and conventional fields in the two countries using *t*-tests with Welch approximation.

of high precipitation (Mucina et al., 2016). As our ordination diagrams suggest, a similar tendency can also be detected within our study area (Figure 3a, c). Our analyses also indicate that other soil variables, like Mg, Ca, K, and humus content, as well as texture still exert some influence on weed species composition (Table 2). This concurs with findings from other country-wide surveys in Hungary (Pinke et al., 2011, 2012, 2013, 2016, 2018, 2022) and other European countries (Vidotto et al., 2016; Nagy et al., 2018; Pätzold et al., 2020). The association of weed flora with these soil parameters is likely to be driven by complex soil chemical interactions with plant functions (White & Greenwood, 2013).

Our survey design also made it possible to compare weed communities at the edges and in the interiors of the plots (plot location), which was also found to be significant in our study (Table 2). This particular variable is neither clearly a management variable, nor a real environmental variable, so we did not include it into any of the main variable groups shown in Table 1 and hence its variance is included among the 'residuals' in Figure 2. This suggests that there was an obvious difference between the weed composition of field edges and field cores. This result seems to be in line with observations previously reported from soybean and oil pumpkin fields in Hungary (Pinke et al., 2016, 2018) and other recent European studies (Wietzke et al., 2020; Yvoz et al., 2021). The influence of plot location on weed distributions can have many explanations. First of all, at field edges, light conditions are usually more favourable than in the inner parts of the fields, dominated by the crop (Seifert et al., 2014). Nonetheless, the stature and density of the crop stands can determine the contrast between field edge and core in terms of light availability, thus influencing the within-field weed distribution patterns (Pinke et al., 2016, 2018). A similar pattern in oilseed rape in France also was confirmed by Berquer et al. (2021), who reported that weed assemblages in field cores are mainly shaped by crop height (indicating crop competition), while height has little effect in the field margins. Additionally, the effects of intensive crop management generally decrease towards the field periphery (Pinke et al., 2012; Wietzke et al., 2020; Yvoz et al., 2021), and the differences between field edge and field core can also be less marked when crop management intensity is lower (Yvoz et al., 2021).

4.3 | Environmental versus management factors

The results of the variation partitioning exercise have shown that the two main groups among the studied variables, the environmental and the management variables, have almost equal influence on the weed vegetation (Figure 2), while both of these groups had a relatively limited overlap with the country. In similar studies for a single crop species in a single country (e.g., Pinke et al., 2016, 2018), environmental variables often account for much more variance than management variables. It is a well-known fact that longer gradients are more 'probable' to exert a statistically significant influence on weed communities (Cimalová & Lososová, 2009; Pinke et al., 2012; Metcalfe et al., 2023). This study had a relatively narrow geographical focus (the borderland region), significantly constraining the environmental gradients in the sample compared to national or continental studies. On the other hand, the presence of the country border with different agricultural systems on the two sides may have extended the management gradients in the sample. This pattern of gradient lengths may have decreased the influence of the environment, and increased that of the management variables in our study, contributing to the balanced relevance of the two main groups of variables that we found. This balanced picture is particularly striking if we consider that only spring-sown crops were sampled in the study, taking away an important source of diversity in management. However, the length of some ecological gradients may also be constrained by the ecological requirements of the surveyed spring-sown crop types (Pinke et al., 2016). Although the six crop species involved in this study have the same sowing season, they are highly diverse in terms of their ecological tolerance and management practices (Doucet et al., 1999; Rauber et al., 2021), which may explain our finding that management exerted approximately the same amount of influence on weed vegetation as the ecological gradients.

4.4 | Influence of the country

Although country is just a single binary variable, it explained a considerable amount of variance in weed composition in this study, even

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compared to the much larger multivariate groups of environmental and management variables (Figure 2). Accordingly, country appeared to be the third most influential predictor in Table 2. Even though our findings did not contradict Metcalfe's observation (that weed communities of a given crop in two different European regions are more similar than those of two different crops within the same region, Metcalfe et al., 2023); we still demonstrated remarkable cross-border differences for most of the crops studied. Surprisingly, most of the variance explained by country was not shared by the other environmental and management variables surveyed. This slightly contradicted our prior expectation that the differences that we can identify in management (different agricultural systems) and environment (different 'topoclimates' and soils) between the two countries will largely explain the differences in the weed communities. As (similarly to altitude) country does not exert a direct influence on weed communities, this finding suggests that there may be several further relevant hidden management or environmental factors that we failed to recognise (or quantify) in this study. These hidden factors may include, for example, several herbicides: unfortunately, our analysis was not able to distinguish the individual active ingredients, even though their use could have been remarkably different between the countries. Due to the high number of different herbicide ingredients their explicit investigation was beyond the aims of this study. Furthermore, with the exception of maize and sunflower, data were collected in different years on the two sides of the border, which means that for the other cultures the effects of country may have been conflated with temporal differences.

Several of the management variables identified as important in our study (including field size, tillage system, tillage depth, farming type, amount of fertilisers, number of herbicides, and preceding crop, see Table 2) were found to differ considerably between the two countries (Table 5, Figure 5). The difference in field size can be considered as the legacy of the centrally governed 'cooperative' system of the Eastern Bloc, which favoured land consolidation and industrialised production, leading to a substantial increase in field sizes in Hungary after the Second World War (Jepsen et al., 2015; Devátý et al., 2019). Our tillage-related findings (that no-tillage was more common in Austria and that primary tillage depth was higher in Hungary) can be related to the lower popularity of conservation agriculture in Hungary (Kertész & Madarász, 2014), which may also be a long-lasting legacy of the centralised and industrialised system in the East. It should be highlighted that the studied drivers are likely to impact weed vegetation in complex ways. For example, smaller fields come with a higher density of field edges and more habitat for edge-preferring species; and no-tillage, as well as organic systems, can indirectly influence the prevalence of several associated management practices. In our study, the amount of fertilisers, as well as the number of herbicides were higher in Hungary, but these differences can probably be attributed to the different frequencies of organic farms, as comparing the two types of farms separately yielded no significant differences between the countries (Figure 6). The considerable difference in the frequency of organic farms (farming type) can also be connected to historical socio-economic legacies. In Austria, organic farming has a long tradition and the organic share of total agricultural land is four and half times larger than in Hungary (Trávníček et al., 2021), which could be also partly due to the lower demands for these products in countries from the former Eastern Bloc (Mazurek-Kusiak et al., 2021). The different frequencies of some previous crops might also be attributed to the distinct crop rotation systems in the contrasting farming types. Former pedological studies on the opposite sides of the former Iron Curtain also identified many divergences in chemical, physical and micromorphological soil parameters, due to different long-term agricultural practices (Rampazzo et al., 1999a, 1999b). Pinke et al. (2019) also highlighted that such agronomical differences are the legacy of the former Iron Curtain, and can still have a lasting impact on weed distribution, as demonstrated in the case of *Ambrosia artemisiifolia*, whose larger abundance on the Hungarian side was also confirmed in this study (Figure 3, Table 4). In addition, this study documented a similar distribution pattern in the case of another weed species, *Abutilon theophrasti* (Table 4); however, this latter species displayed more ambiguous country preferences, as it was more abundant in Hungarian maize and pumpkin fields but showed a contrasting preference in sugar beet (Table 4). Both of these species are on the list of the most noxious alien weeds in Austria (Follak et al., 2017), and the abrupt change in their distribution along the borderline may also be explained by a combination of environmental, agronomical, and historical reasons. The influence of historical factors on species composition was also demonstrated by studies from other parts of the previous Iron Curtain zone, for example, the Czech–Austrian and the East–West German borderlands, where the legacies of historical land-use regimes still exert observable influence on the present farmland bird diversity (Batáry et al., 2017; Šálek et al., 2021; Noack et al., 2022).

5 | CONCLUSIONS

Our study revealed that country exerts a small yet clear influence on weed communities in the studied historical borderline region, which can only partially be explained by management and environmental variables. Beyond country, preceding crop and actual crop were ranked as the two most important variables, principally based on the impact of different sowing time and architecture-related aspects. The topoclimatic differences along the borderland also have a strong environmental signature on the weed vegetation. Nevertheless, the distinct historical backgrounds of the two countries, including the legacies of the Iron Curtain era, seem to have a lasting impact on the species composition of arable fields. While our results did not contradict the general observation for European weed communities, that inter-crop differences (within a region) are much larger than regional differences (for the same crop), we still documented the existence of remarkable cross-border differences for five major crop species. Accordingly, our

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study demonstrates that, as a complement to 'big data' analyses of large-scale macro-ecological databases, regional surveys with intensive sampling strategy can also further our understanding of vegetation organisation, especially where large gradients are mixed with historical legacies.

AUTHOR CONTRIBUTIONS

Gyula Pinke, Zoltán Botta-Dukát and Bálint Czúcz conceived of the research idea; Gyula Pinke, András Vér, Krisztina Réder, Gábor Koltai, Gerhard Schlögl and Ákos Bede-Fazekas collected data; Zoltán Botta-Dukát performed statistical analyses; Gyula Pinke, with contributions from Ákos Bede-Fazekas, Zoltán Botta-Dukát and Bálint Czúcz, wrote the paper; Bálint Czúcz revised and finalised the article; all authors discussed the results and commented on the manuscript.

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DATA AVAILABILITY STATEMENT

The data sets are available from: https://doi.org/10.5281/zenodo.10397240.

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SUPPORTING INFORMATION

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

Appendix S1. Supplementary figures and tables.

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