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Ancient mounds, modern refuges: Out-of-production sites on kurgans support rare weeds in agricultural landscapes

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ABSTRACT

Rare weeds (RW) are disturbance-tolerant plants that enhance agrobiodiversity and related ecosystem services without adversely affecting agricultural production. However, due to agricultural intensification, RWs are declining across Europe, and their conservation requires targeted measures addressing their special ecological requirements. We aimed to explore the potential of out-of-production sites for maintaining populations of RWs characteristic of arable lands, old-fields, and grasslands. In an intensive field survey, we collected data from 216 sites in Hungary, including sites covered with spontaneously recovering grassland vegetation and reference grasslands. We aimed to identify site- and landscape-specific factors (i.e., geographic position, landscape transformation, habitat area, environmental heterogeneity, soil properties, age of the vegetation, and other vegetation attributes) influencing the occurrence and species richness of RWs. We recorded 38 RW species, including 15 red-listed and two protected ones. RWs occurred on 50.9 % of the study sites, indicating that out-of-production sites can provide refuge for RWs associated to croplands, old-fields, and grasslands. Environmental heterogeneity was the most important factor supporting the occurrence of RWs, particularly grassland-related RWs. Poisson models revealed that the total number of RW species was lower in northern sites. The number of arable RWs was higher in sites with high soil $CaCO_3$ content, while high soil phosphorus content supported fewer grassland RW species. Sites with diverse vegetation harboured more old-field and grassland RWs. Land sparing through the maintenance of out-of-production sites and supporting environmental heterogeneity and establishment gaps can contribute to the conservation of RWs in agricultural landscapes.

1. Introduction

Transformation of natural and semi-natural ecosystems into croplands is one of the major threats to global biodiversity. Grassland ecosystems with fertile soils have been especially affected by land conversion since the Neolithic (Albrecht et al., 2016). This process accelerated significantly in the past two centuries due to increased food demands of the exponentially increasing human population, and technical advances enabling unprecedented land use intensification (Biró et al., 2018; Potapov et al., 2022; Schmid et al., 2017). Such changes led to the reduction and isolation of remaining grasslands, severely threatening the flora and fauna of open landscapes (Schmid et al., 2017).

In Europe, agricultural intensification and related land-transformation accelerated after World War II, causing dramatic landscape-level shifts in species composition and a general decline in plant diversity of agroecosystems (Lososová et al., 2004; Twerski et al., 2022). These trends particularly affected species adapted to traditional, extensive land-use practices (Albrecht et al., 2016). However, agroecosystems comprising croplands and semi-natural habitats can still sustain high biodiversity, including rare and endangered species in

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many European countries (Pinke and Gunton, 2014; Rotchés-Ribalta et al., 2015a; Tscharntke et al., 2005). Besides its conservation relevance, agrobiodiversity contributes to the delivery of ecosystem services (such as pollination, biological control, carbon sequestration, and water retention) essential for the humankind (Tscharntke et al., 2005; Twerski et al., 2022).

Agroecosystems hold many plant species adapted to frequent soil disturbance related to arable use or trampling and frequent biomass removal in grazed grasslands (Pellaton et al., 2023; Twerski et al., 2022). Some of these disturbance tolerant species can be considered problematic weeds, because due to their high biomass, good competitive ability for light, and specific traits (such as high regeneration ability, herbicide resistance, tolerance to or avoidance of grazing) they can reduce crop yields or decrease fodder quality (Bourgeois et al., 2019; DiTomaso, 2000). However, some other non-crop, disturbance-tolerant plants referred to as rare weeds (RW) can enhance agrobiodiversity and related ecosystem services without harming agricultural production (Storkey et al., 2012). These species are typical of extensively managed croplands, old-fields, and grasslands, and have become rare due to the intensification of agricultural practices (Zerbe, 2023).

RWs can be categorized into ecological groups based on habitat preference. Arable RWs require regular soil disturbance, have poor herbicide-resistance, and due to their low competitiveness, they prefer open habitats with low vegetation cover (Storkey et al., 2012). Although primarily arable RWs are confined to extensive croplands, they can also become established in fallows and field margins (Fried et al., 2009). In old-fields and grasslands, there are also several rare, disturbance-tolerant weedy species (old-field RWs and grassland RWs) of high conservation importance, which are often supported by small-scale disturbances, such as those created by extensive grazing (Pellaton et al., 2023).

Like weeds in general, the distribution of RWs is considerably influenced by climatic factors, such as mean annual temperature and precipitation, which correlate well with geographical position (Fried et al., 2008) (Table 1, Appendix Table 1). The RW flora of agroecosystems depends on factors acting at both site (parcel or grassland) and landscape levels (landscape composition and structure) (Kovács-Hostyánszki et al., 2013). At the site level, intensive agricultural practices have been adopted in many formerly extensively managed croplands (e.g., cessation of crop rotation, use of heavy machinery, excessive tilling, improved seed cleaning, using higher crop densities, and the application of large amounts of synthetic fertilisers and herbicides) to increase yield (Kovács-Hostyánszki et al., 2013; Storkey et al., 2012; Twerski et al., 2021). Although one of the main goals of these practices was to control competitive weeds, they instead suppressed species that posed a low threat to yield production but had a high

Table 1
The hypothesised effects of the studied factors on the occurrence probability and species richness of rare weeds.

Factor	Measure	General effect	Hypothesised effect on rare weeds	Citation
geographic position	northing, easting	geographic position directly influences climatic factors, such as temperature, which in turn affect the composition of weed communities	colder climate in northern areas may limit the establishment of thermophilous RWs	Fried et al., 2008
level of landscape transformation	percentage of arable lands in the neighbouring landscape	high percentage of arable lands in the landscape indicates intensive land use and high level of landscape transformation, both of which negatively impact the landscape-level species richness and the species richness of species typical of semi-natural habitats	species richness of arable RWs is higher, while that of old-field and grassland RWs is lower in landscapes with a high proportion of arable lands	Rotches-Ribalta et al., 2015b; Prangel et al., 2023
	distance to the nearest grassland; percentage of grasslands in the neighbouring landscape; Hanski connectivity index	high percentage and connectivity of grasslands indicates an extensive land use and a low level of landscape transformation; functional connections among semi-natural habitats promote landscape-level species richness and species richness of species associated with semi-natural habitats	species richness of old-field and grassland RWs is higher in less transformed landscapes with a high proportion of grasslands	Brückmann et al., 2010; Deák et al., 2021a
habitat area	total area of the site	larger areas support the establishment of a greater number of species	larger sites support a greater number of RWs	MacArthur and Wilson, 1967
environmental heterogeneity	topography (relative height)	topographically more heterogeneous sites are characterised by greater environmental heterogeneity, which enhances the coexistence of species with diverse environmental preferences	presence of contrasting microsites promotes the coexistence of RWs with differing environmental preferences and life strategies	Stein et al., 2014; Deák et al., 2021b
soil nutrients (N, P, K)	soil N, P, K content	increased soil nutrient levels lead to higher productivity and dominance of competitive plant species	increased soil nutrient levels reduce RW species richness due to increased level of competition	Pinke and Gunton, 2014; Storkey et al., 2012
soil texture	Arany-type plasticity index	agricultural practices are less intensive on poor sandy soils compared to fertile loamy soils	less intensive land use practices allow RWs to establish more successfully	Fried et al., 2008; Pinke et al., 2012
soil chemical reaction	$CaCO_3$ content of the soil	high $CaCO_3$ concentrations and the resulting high soil pH increase species richness during secondary succession	species richness of RWs increases with higher soil $CaCO_3$ content and related higher pH	Lososová et al., 2004; Sojneková and Chytrý, 2015
successional stage	number of years since abandonment from arable use	with increasing age, community assembly shifts from disturbance-tolerant species to more competitive ones	species richness of arable RWs is higher at sites in younger successional stages, whereas old-field and grassland RWs dominate sites with older successional stages	Prach et al., 2014
canopy openness	total vegetation cover	closed canopy creates strong competition for light and reduces the availability of open establishment gaps	sites with lower total vegetation cover can support more RWs	Kleijn and van der Voort, 1997
diversity of the vegetation	Shannon diversity of the vegetation	in the absence of dominant competitor species, competition levels are lower in more diverse communities	diverse communities host more RWs with low competitive abilities	Prach et al., 2014
naturalness of the vegetation	community weighted mean of species (Social Behaviour Type scores)	high naturalness values indicate the presence of well-established, closed grassland vegetation	in late successional vegetation RWs are suppressed	Prach et al., 2014

contribution to biodiversity (Rotchés-Ribalta et al., 2020). At the same time, in grasslands, the cessation of extensive grazing and mowing caused litter accumulation and dominance of a few strong competitor herbaceous or woody species that pose a serious threat to several disturbance-tolerant grassland plants confined to open gaps (Prangel et al., 2023; Valkó et al., 2018).

Landscape-scale land consolidation actions considerably rearranged the structure of agricultural landscapes that also severely affected RWs (Albrecht et al., 2016). Merging small parcels into larger ones simplified landscapes, reduced crop diversity and also decreased habitat diversity and environmental heterogeneity, by the elimination of field margins, road verges, hedgerows, and other semi-natural habitats that previously supported all ecological groups of RWs (Fried et al., 2009; Rotchés-Ribalta et al., 2015a; Storkey et al., 2012). These effects were most pronounced in landscapes with fertile loamy soils, and less intense on poor sandy soils with low agricultural potential (Fried et al., 2008). Such transformations led to a drastic decline in the populations of formerly widespread and abundant RW species making them highly endangered in many European agroecosystems (Pinke and Gunton, 2014; Storkey et al., 2012). Consequently, many RWs are now included in regional red lists (Pinke et al., 2011; Rotchés-Ribalta et al., 2015b). For instance, 35 %, 28 %, and 28 % of the arable flora are endangered in Germany (Korneck and Sukopp, 1988), the Netherlands (Kleijn and van der Voort, 1997), and England (Stroh et al., 2014), respectively. Pinke et al. (2011) listed 149 endangered RW species confined to croplands, ruderal habitats, wetlands, and dry habitats of Hungary which represents 5.8 % of the country’s flora.

At the European level, in order to halt arable RW decline, several targeted conservation actions have been initiated including RW-friendly arable systems, and sowing of arable RW species in agricultural lands (Twerski et al., 2021; Zerbe, 2023). In contrast, conservation actions targeting grassland species often focus on rare “flagship” habitat specialist species of well-preserved natural or semi-natural grasslands (see e.g. the list of plant species with community interest in the Annex II of the EU Habitats Directive) and species of early- and mid-successional habitats are seldom considered. Thus, despite their endangered status, old-field and grassland RWs receive limited attention.

Recognising the negative consequences of land-use intensification, the importance of biodiversity protection, and the positive correlation between biodiversity and ecosystem services, certain agri-environmental schemes (AESs) funded by the Common Agricultural Policy (CAP) of the European Union support farmers reducing the management intensity on their lands. Within this framework, among other measures, the establishment of out-of-production sites that are completely removed from agricultural production is subsidised. These areas allow spontaneous secondary old-field succession, which can support biodiversity, enhance pollination and pest control services, and preserve landscape structures. In the initial years after abandonment, these regenerating areas are typically characterised by weed-dominated fallow vegetation. Over time, under optimal conditions there is a gradual decline in ruderal species, and the vegetation can spontaneously develop into an old-field composed by grassland-related species (Prach et al., 2014; Schmid et al., 2017; Sojneková and Chytrý, 2015). Considering the ecological requirements of arable, old-field, and grassland RW species, they might prefer successional vegetation of different ages.

We aimed to explore the potential of out-of-production sites in maintaining populations of RWs belonging to three ecological groups: those characteristic of arable lands, old-fields, and grasslands. For this, we conducted an intensive field survey and collected data from a total of 216 sites in Hungary, covered with spontaneously recovering grassland vegetation and reference grasslands. We also aimed to identify site- and landscape-specific factors influencing the presence and species richness of RWs in these sites (Table 1). In particular, we focused on the effects of geographic position, landscape transformation, habitat area, environmental heterogeneity, soil properties (nitrogen, phosphorus, potassium, calcium carbonate content, and soil texture), age of the vegetation (time since abandonment), and other vegetation attributes (naturalness, Shannon diversity, and total vegetation cover).

We hypothesised that:

(i) The occurrence probability and species richness of rare weed species in all ecological groups (arable, old-field, and grassland RWs) are higher in sites with a larger area, holding a high environmental heterogeneity, characterised by soils with coarser texture and low nutrient content, having a high calcium carbonate content, covered with a diverse vegetation with a low cover.

(ii) Arable RWs are typical of landscapes characterised by a high proportion of croplands, and confined to sites that were recently abandoned from ploughing, and are characterised by ruderal vegetation.

(iii) Old-field and grassland RWs occur in less transformed landscapes characterised by high proportion and connectivity of grasslands, and in sites with natural-like late-successional herbaceous vegetation situated in moderately transformed landscapes.

2. Materials and methods

2.1. Study area

Our study area, covering approximately 21,500 km^2, is located in the Great Hungarian Plain in eastern Hungary. We focused on the lowland regions bordered by the Tisza River, the North Hungarian Mountains, and the sandy areas of Nyírség and the Bihar Mountains, as this region represents a relatively uniform landscape in terms of flora and vegetation. The elevation in this lowland landscape ranges from 76 to 120 m asl. The climate is temperate continental. The annual precipitation is between ranges from 498 to 565 mm, and the mean annual temperature ranges from 10 to 11 °C (Fick and Hijmans, 2017).

Historically, the area was dominated by vast dry grasslands (Biró et al., 2018). Large-scale conversion of natural habitats to croplands began in the Medieval period, and accelerated during the 18th and 19th centuries, when huge proportions of grasslands were lost due to agricultural intensification and urbanisation (Biró et al., 2018). Further habitat loss occurred after World War II, during collectivisation, which led to the tilling of additional grasslands (Deák et al., 2021b). Today, the region is predominantly characterised by intensively managed croplands making our study system a good representative of Central European lowland agricultural landscapes.

In the studied landscape, remnants of semi-natural vegetation usually persist as small, fragmented grassland patches, road verges, and kurgans (ancient, millennia-old burial mounds; Deák et al., 2023). Kurgans constructed during the Copper and Bronze Ages are typical and widespread landscape elements of the Eurasian steppe and forest steppe biomes. Their documented number exceeds half a million (Deák et al., 2023). However, as official data sources are predominantly based on a few regional-level surveys covering only a small proportion of the geographic area containing kurgans, it can be assumed that the actual number of kurgans is much larger. Although many kurgans have been ploughed during the past centuries, intact kurgans still function as safe haven for grassland-related plants, and harbour high biodiversity (Deák et al., 2021a, 2021b). As kurgans are essential parts of the Hungarian lowland landscapes, and represent important cultural values, they were integrated in the single area payment scheme of the CAP in 2010 as protected landscape elements. Beneficiaries applying for subsidies should avoid any harmful activities (i.e., soil disturbances related to arable farming or silviculture on the kurgans. Consequently, kurgans located on subsidised parcels serve as out-of-production sites. Although farmers could gain subsidies for kurgan protection since 2010, the abandonment of arable use on kurgans occurred gradually even before and after 2010, resulting in a broad range of successional vegetation of different ages. In most cases, kurgans are left to spontaneous grassland succession. Active restoration or management measures are seldom applied on them due to their inaccessibility within agricultural parcels.

This practice potentially supports RW species typical of extensively used arable lands, old-fields, and grasslands. As kurgans situated within agricultural parcels are generally covered with fallow, old-field, or semi-natural grassland vegetation, they can be proper objects for studying the potential of out-of-production sites in RW conservation.

2.2. Study sites

We selected 216 sites (i.e., kurgans), including 192 formerly ploughed out-of-production sites and 24 sites holding millennia-old (approximately 5000-year-old) grasslands (Fig. 1). All sites were embedded in agricultural landscapes with varying proportions of cropland within a 300-meter buffer around each focal patch (range 0–99.5 %; mean 70.0 % ± 27.1 SD). Area of the sites ranged from 90 to 16,942 m^2 with a mean area of 3258.6 m^2 ± 2774.0 SD. Out-of-production sites were covered with spontaneously recovering vegetation, exhibiting a large variation in age (from one to 144 years). We selected sites where, after cessation of arable use, vegetation recovery occurred passively, without any kind of restoration measures such as seeding, mowing, grazing or herbicide application. To estimate the age of the secondary vegetation, we used time series of satellite images from Google Earth (Google Earth, 2024), archival aerial photographs (source: www.fentrol.hu), and topographic maps: Second (1858–1864) and Third (1881–1884) Military Survey of the Hungarian Empire, the Military Survey of the Hungarian People's Republic (1956–1975) and the actual topographical map of Hungary (Institute and Museum of Military History, Budapest). Since kurgans have been key orientation points in the otherwise homogenous flat landscapes, their locations and land cover were consistently represented on these maps. Previous studies have shown that mound height positively correlates with environmental heterogeneity, which is an important driver of plant diversity (Deák et al., 2021b). To account for the potential effects of environmental heterogeneity on RW presence and richness, we selected kurgans of varying heights (0.2–7.8 m, mean 3.0 m ± 1.6 SD).

2.3. Field surveys

2.3.1. Botanical survey

The botanical survey was conducted over three years (2021–2023). Each site was surveyed once during the peak of the vegetation season (May or June). At each site we recorded the list of vascular plant species and visually estimated the total percentage cover of each species. For recording the species lists of vascular plants, we applied a visual survey of the whole site. As part of a standard protocol, three surveyors spent 30 min per 0.1 ha during the survey. We decided to consider the whole site as one sampling unit, since the sparse distribution and low coverage of RWs made classical survey methods using random plots less effective because of the high chance for missing species represented by only a few individuals.

2.3.2. Habitat mapping

In parallel with the botanical survey, we prepared habitat maps within a 300-meter buffer around each site using satellite images from Google Maps (Google Maps, 2024) and Bing Maps (Bing Maps, 2024). We mapped croplands and grasslands around the studied sites. During the mapping we also recorded the central coordinates of each site with a handheld GPS.

2.3.3. Soil sampling and analysis

After removing litter, we collected a pooled 1000 cm^3 soil sample from the top 10 cm of the soil of the north-, east-, south-, and west-facing slopes and the top of each mound. The soil samples were air-dried, and homogenised.

The amount of nitrogen (NO_2^- and NO_3^-), phosphorus (expressed by

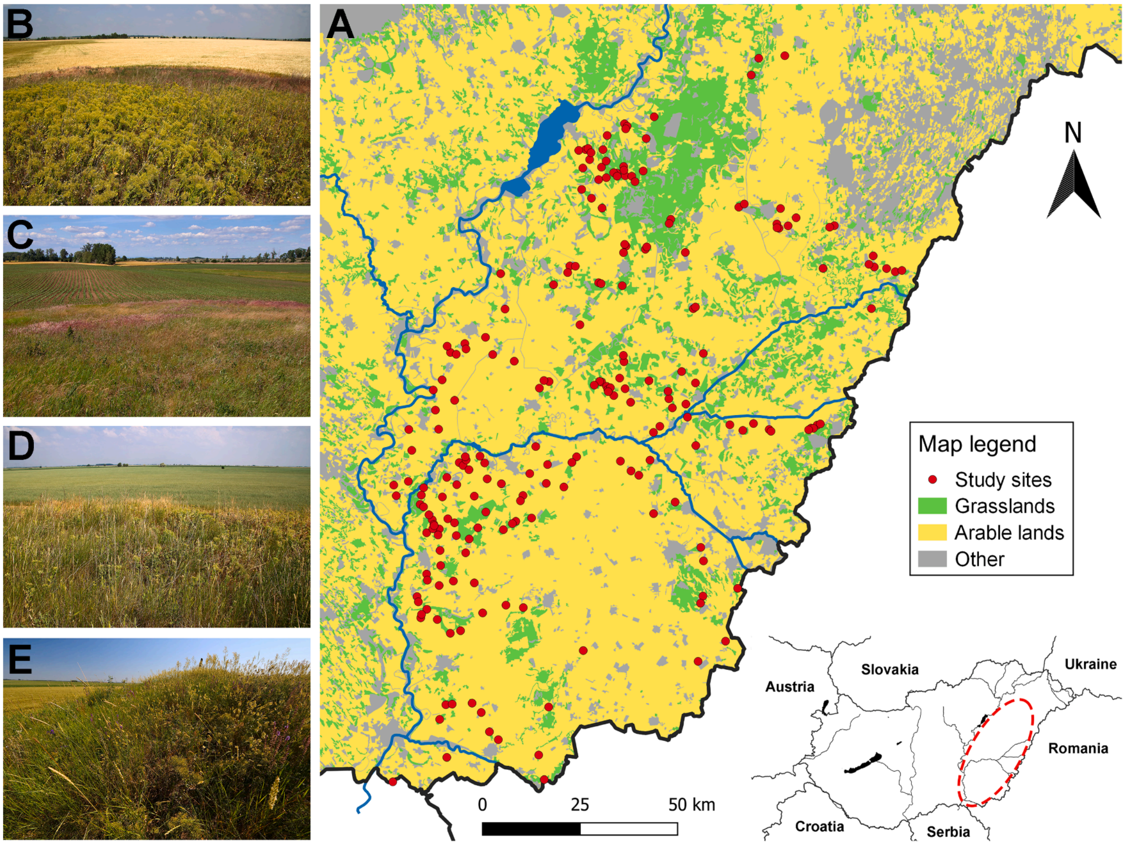


Fig. 1. Map of the study area and the sites studied (N = 216 kurgans). Photos on the left illustrate typical successional vegetation of different ages. Notations: A – Young fallow (4 years old); B – Old-field (11 years old); C – Old-field (61 years old); D – Ancient semi-natural grassland. Photo credits: Balázs Deák.

P_2O_5), potassium (expressed by K_2O), and $CaCO_3$ content of the soil were analysed in an accredited laboratory (reference number: NAH-1–1437/2018). For the assessment of soil texture, soil samples were homogenised, and the "Arany type plasticity index" (PA) was measured (MSZ-08 0205, 1978). This index refers to the following soil texture categories: PA < 25 coarse sand; PA = 25–30 sand; PA = 31–37 sandy loam; PA = 38–42 loam; PA = 43–50 clay loam; PA = 51–60 clay; and PA > 60 heavy clay soils.

2.4. Data processing

2.4.1. Species data

In this study, we focused on RW species that can spontaneously occur in out-of-production sites embedded within agricultural landscapes. For this, we defined criteria for rarity itself and for rare weed strategy. It was necessary, as although there are many published studies focusing on rarity and weed strategy, currently there is no universal definition for RWs. Existing definitions are largely context-dependent, varying by scientific field, geographical region, and practical considerations. In our study, we considered conservation and ecological aspects when assigning species to groups.

The rarity of a species depends heavily on geographical context (Pinke et al., 2011), which can vary even within the same country (e.g., lowlands vs. hilly areas). Although national-level red lists provide a good overview of species rarity based on overall occurrence data, for practical considerations rarity should be rather evaluated at the regional level to better reflect the local conditions of a specific area. Thus, we used the current distribution data of each species within the studied region as a proxy of rarity. For this, we used the Distribution Atlas of Vascular Plants of Hungary (Bartha et al., 2015), which provides a comprehensive and regularly updated floristic dataset including data provided by the Hungarian Flora Mapping Programme, herbarium data, and data derived from scientific publications. In the Distribution Atlas of Vascular Plants of Hungary occurrence data are represented in 2827 grid cells (c.a. 6.3 km × 5.6 km) which align with the Central European Flora Mapping System. Our study area is covered with 594 grid cells. We considered a species rare, if it occurred in less than 25 % of the grid cells in the study area. Most of these species became rare in the near past, and generally exist in small populations (Pinke et al., 2011). It is important to emphasise that in certain cases, local rarity does not reflect the frequency of a species' distribution at larger geographical scales. In our dataset, *Vulpia myuros* and *Centaurea solstitialis* can be considered rare weeds based on their occurrence data within the studied region. However, it should be noted that in the western, more humid regions of Hungary, *Vulpia myuros* was recently classified as a pernicious weed. The persistence of this species is due to its herbicide resistance, which can be particularly problematic in no-till systems (Ughy, 2017). Additionally, while *Centaurea solstitialis* is a red-listed and protected species in Hungary, it is considered invasive in the USA, often forming dense monodominant stands and significantly reducing forage quality in pastures (Eagle et al., 2007).

We defined RWs as species that (i) can became established spontaneously (without sowing), (ii) are adapted to intense and recurring disturbance regimes, (iii) require open gaps for long-term survival, (iv) are subordinate/casual species with low competitive ability, (v) do not dominate or transform their habitats (vi), and do not negatively affect crops or grassland species (Storkey et al., 2012; Zimdahl and Basinger, 2024). Thus, it is important to emphasise that RWs studied here, are not typical weeds in an agricultural sense.

Finally, we categorized species that meet the criteria for being an RW into three ecological groups: arable RW, old-field RW, and grassland RW species (Appendix Table 2). Habitat specificity was based on the species descriptions by Király (2009), which were adjusted using field observations by the authors of this paper to better reflect the characteristics of the study area. Taxonomic nomenclature followed Király (2009).

2.4.2. Vegetation data

We calculated the Shannon diversity of the vegetation for each site. To assess the overall conservation status of the sites, we calculated a naturalness score. The naturalness score was based on the cover-weighted mean social behaviour type (SBT) scores of each species. The SBT system is based on the model by Grime (1979) that was adapted for Hungarian conditions by Borhidi (1995). The naturalness score describes the role of individual species in communities, and the community level cover-weighted mean of SBT scores provides information on the degree of disturbance, regeneration ability, and stability of the vegetation. SBT system classifies species into functional groups: specialists (+6), natural competitors (+5), generalists (+4), natural pioneers (+3), disturbance-tolerants (+2), weeds (+1), introduced species (-1), ruderal competitors (-2), and adventive competitors (-3). When calculating naturalness scores and Shannon diversity, we excluded RW species, since both scores were used as explanatory variables of RW occurrence in the models.

2.4.3. Habitat maps and connectivity indices

Habitat maps were digitised, and the areas of arable lands and grasslands were calculated using QGIS software (QGIS Development Team, 2022). We also measured the edge-to-edge distance between the focal habitat patch and the nearest grassland stand using a habitat map prepared in the field. If grasslands were absent within the 300-meter buffer, we used satellite images from Google Maps (Google Maps, 2024) and Bing Maps (Maps, 2024) to identify the nearest grassland habitat. To estimate the connectivity of grassland habitats within the 300-meter buffer, we used the Hanski connectivity index (Hanski et al., 2000). We set the α parameter, which is related to dispersal ability, to 5, corresponding to a dispersal distance of 200 m, as RW species often exhibit low dispersal ability (Storkey et al., 2012). The β parameter, which describes the scaling of immigration, was set to 0.5.

2.4.4. Statistical analyses

We built zero-inflated generalized linear mixed models (GLMMs) to study the impact of environmental and land use factors on the occurrence and species richness of RWs. Since RWs are generally present with a low abundance exhibiting a negligible level of between-species variance, in the models we used only the total RW species richness, and species richness of arable-, old-field-, and grassland-related RWs as dependent variables. Hence, four independent GLMMs were built. The models consisted of a zero-inflation model part, which accounted for the impact on the RW occurrence, and a Poisson model part, which accounted for the residual impact on the RW richness. To eliminate the effect of the interannual variability of species detection, the survey year was treated as random factor in the models.

We applied a two-step filtering on the 17 environmental and land use factors collected for the analysis (Appendix Table 1). First, we created a subset of the factors that fulfilled our multicollinearity criteria: pairwise Pearson's and Spearman's correlation coefficients were limited to $|r| < 0.6$ and $|\rho| < 0.6$, respectively, Variance Inflation Factor (VIF) of the variables were maximized at 5, and Condition Number (CN) of the variable set was maximized at 10 (Dormann et al., 2013). During dropping the factors violating the criteria, we sought to ensure that the factors retained describe the four main environmental characteristics (i.e., landscape, soil, vegetation, and site-related characteristics) in as balanced a way as possible and that as many of the relationships known from the literature as possible are retained. As a result of this filtering step, 14 factors were retained with $\max(|r|) = 0.51$ (between phosphorus and potassium; Appendix Table 3), $\max(|\rho|) = 0.53$ (between northing and easting; Appendix Table 4), and $\max(\text{VIF}) = 2.17$ (age; Appendix Table 5). The Condition Number of the resulting subset of the factors was 3.13.

As a second filtering step we applied forward factor selection for the four GLMMs independently. Starting from the intercept model, fixed factors were added to the model formula iteratively until the best model was found according to the Akaike Information Criterion (AIC; Akaike, 1974). In each iteration, the selection of the one factor that improves the model the most was done for the zero-inflation model part and the Poisson model part separately following our hypothesis that occurrence and richness of RWs might be driven by different factors. Thus, the final model contained the same number, but possibly different list of fixed factors in its two model parts.

While we retained coordinates, i.e., northing and easting, in the first filtering step, the second filtering step might remove these factors from some of the models. Hence, spatial structure might not always be directly included in the models. To study whether spatial patterns unexplained by the selected fixed factors still remain in the residuals, residual spatial autocorrelation was measured with Moran's I (Moran, 1950). All statistical analyses were conducted in R statistical software (R Core Team, 2024) using the packages “ape” (Paradis and Schliep, 2019), “car” (Fox and Weisberg, 2019), “corrplot” (Wei and Simko, 2021), "ICEbox" (Goldstein et al., 2015), “glmmTMB” (Brooks et al., 2017), and “Hmisc” (Harrell, 2022).

3. Results

We found altogether 38 RW species. Among these there were two species listed in the IUCN Red List, 13 species included in the Hungarian Red List (Király, 2007), and two were protected species (Appendix Table 2; Fig. 2). The detailed description of locations where species were found was published in our floristic data paper (Süveges et al., 2025). We identified 20 species with a Mediterranean, Sub-Mediterranean, or Pontic origin according to the geographic area distribution categories of Horváth et al. (1995). Out of the 216 study sites, 106 sites did not hold any RW species. 67 sites held one species, 26 sites held two, 11 sites held three, three sites held four, one site held five, and two sites held six RW species (Fig. 2).

Zero-inflation model parts of the best models fitted on occurrence data of arable, old-field, grassland, and total RWs separately revealed only one significant factor (Fig. 3; Appendix Table 6). Increased mound height decreased the likelihood of RW species occurrence (negative value of the coefficient in the zero-inflated component indicates that higher values of the factor decrease the likelihood of excess zeros). Poisson models showed that the total number of RW species was lower in northern sites (Fig. 4), primarily due to a decrease in old-field and grassland RW richness (Figs. 5 and 6). Sites with higher environmental heterogeneity held more grassland RW species. Total number of RWs was also higher in such sites. Larger sites were associated with lower species richness of old-field and grassland RWs, which decreased the

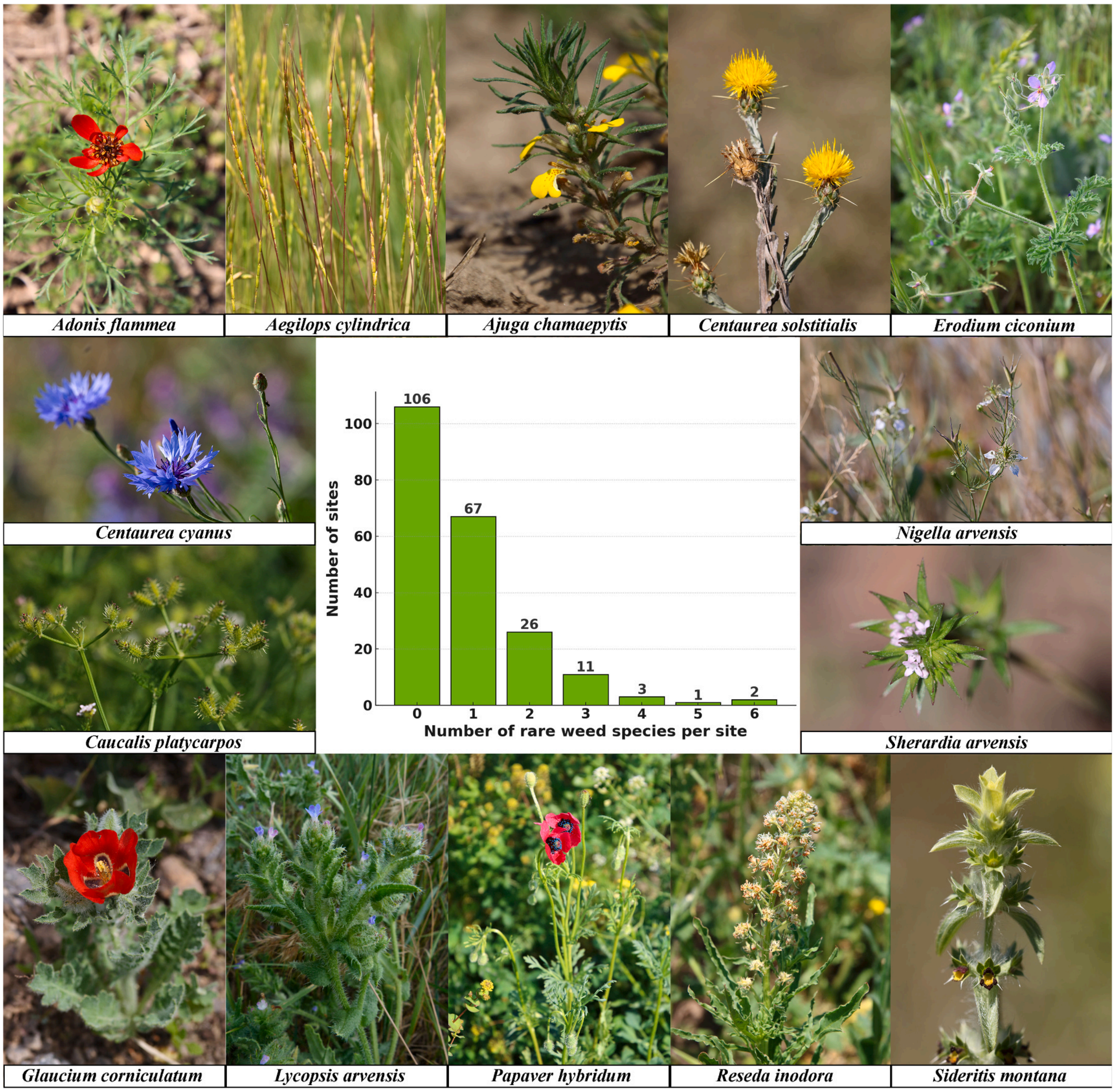
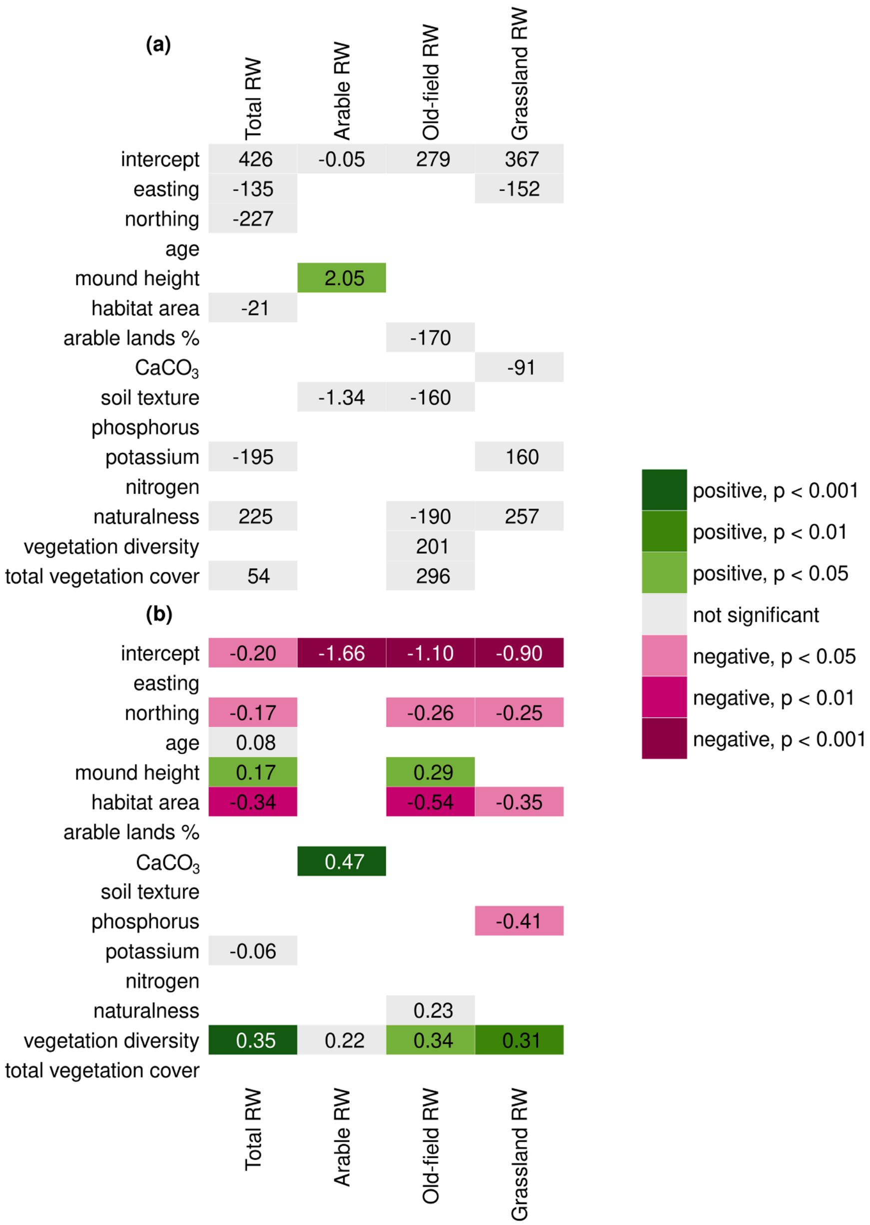


Fig. 2. Frequencies of RW species in the studied sites, and photos of some representative RW species. Photo credits: Balázs Deák and Laura Godó.



(a)

	Total RW	Arable RW	Old-field RW	Grassland RW
intercept	426	-0.05	279	367
easting	-135			-152
northing	-227			
age				
mound height		2.05		
habitat area	-21			
arable lands %			-170	
$CaCO_3$				-91
soil texture		-1.34	-160	
phosphorus				
potassium	-195			160
nitrogen				
naturalness	225		-190	257
vegetation diversity			201	
total vegetation cover	54		296	

(b)

	Total RW	Arable RW	Old-field RW	Grassland RW
intercept	-0.20	-1.66	-1.10	-0.90
easting				
northing	-0.17		-0.26	-0.25
age	0.08			
mound height	0.17		0.29	
habitat area	-0.34		-0.54	-0.35
arable lands %				
$CaCO_3$		0.47		
soil texture				
phosphorus				-0.41
potassium	-0.06			
nitrogen				
naturalness			0.23	
vegetation diversity	0.35	0.22	0.34	0.31
total vegetation cover				

Fig. 3. Effects of site- and landscape level variables on the occurrence possibility and species richness of all rare weeds (total RW), and arable land (arable RW), old-field (old-field RW) and grassland-related (grassland RW) rare weeds (zero-inflated GLMMs with backward model selection; N = 216). The results of the zero-inflated (panel 'a') and Poisson models (panel 'b') are shown separately. Significant effects ($p < 0.05$) are marked with boldface.

total RW richness too. Arable RW species number was higher in sites with high soil $CaCO_3$ content, whereas sites with high soil phosphorus content supported fewer grassland RW species (Fig. 7). Sites with diverse vegetation had higher species richness of old-field and grassland RWs.

Residual spatial autocorrelation of the models of total RW, arable RW, old-field RW and grassland RW was 0.018, 0.001, 0.010, 0.011, respectively, according to the Moran's I. Each of these values were close to zero and not significant at $\alpha = 0.05$ significance level suggesting that the spatial patterns unexplained by the selected fixed factors are negligible.

4. Discussion

Our results showed that out-of-production sites can provide refuge for RWs confined to croplands, old-fields, and grasslands in agricultural landscapes. Interestingly, mound height, which is a proxy of environmental heterogeneity, was the only significant predictor of RW species' occurrence. However, when RWs were present at a certain site, large variety of factors such as habitat area and mound height, nutrient and calcium carbonate content of the soil, and also the Shannon diversity of the vegetation had a considerable effect on their species richness.

We found high numbers of red-listed RW species in our study sites; however, it should be noted that in general the frequency of individual species was low. 50.9 % of the sites held RW species, and RW species had an average frequency of 2.2 %. This aligns with the findings of Rotchés-Ribalta et al. (2015b) who reported that in their studied sites 70 % of RWs occurred with frequencies below 5 %. In our study, we detected seven arable RW species, while RW species of old-fields (14 species) and grasslands (17 species) were represented in larger numbers. Since these species groups are among the "losers" of global agricultural intensification and often remain a conservation blind spot, their survival and protection are critically important.

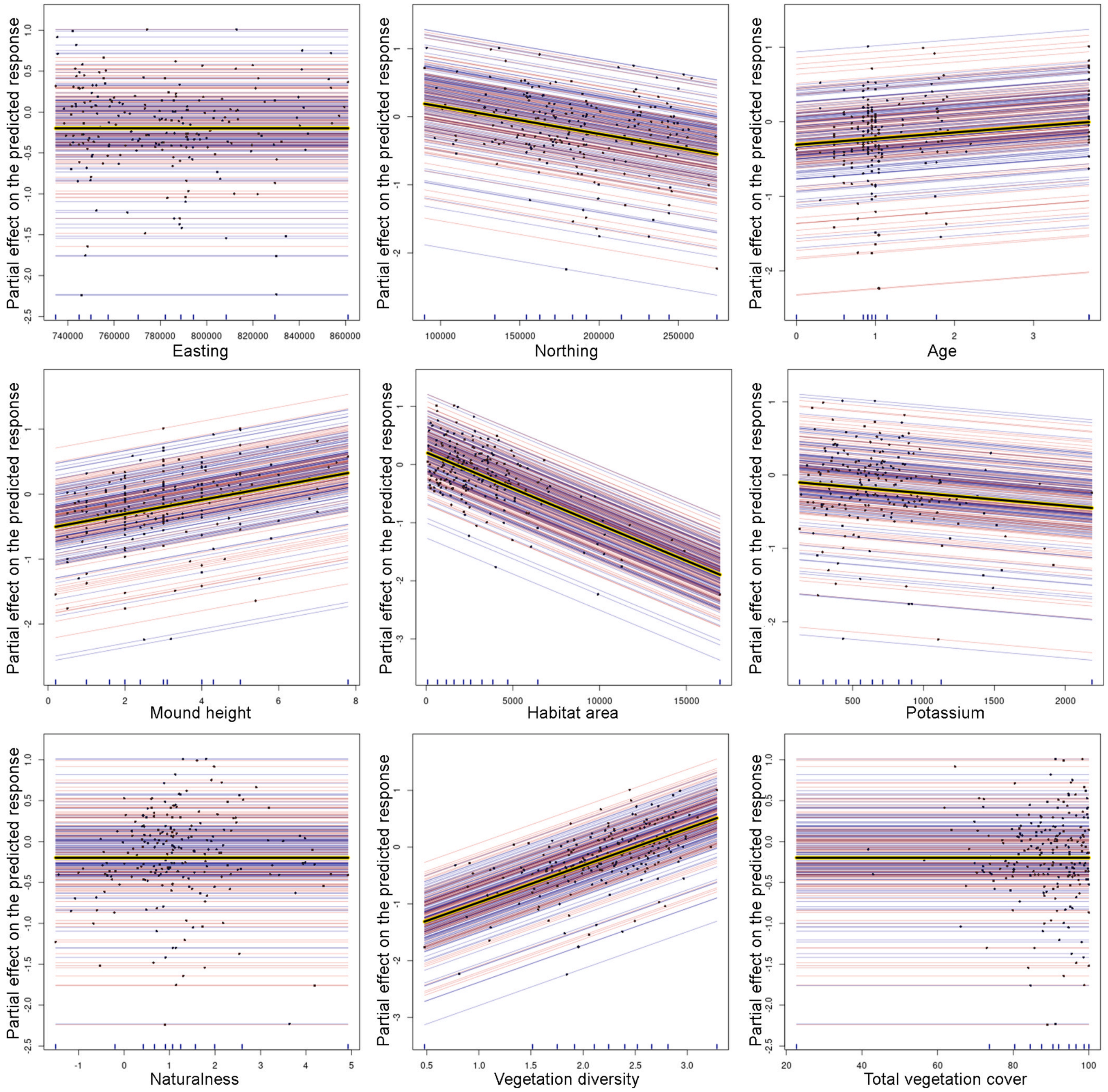


Fig. 4. Individual conditional expectation curves illustrating the effects of factors retained in zero-inflated GLMMs, selected through forward factor selection, calculated for all rare weeds. Notations: red lines – curves calculated for sites without rare weeds; blue lines – curves calculated for sites holding ≥1 rare weed species; bold black line with a yellow highlight – partial dependence plot, mean of the individual conditional expectation curves.

4.1. Geographic position

Many RW species (53 %) present in the studied sites (such as *Androsace elongata*, *Calepina irregularis*, *Nigella arvensis*, and *Trifolium diffusum*) had a Mediterranean, Sub-Mediterranean and Pontic origin (Horváth et al., 1995). Other European studies also noted that Mediterranean species are well-represented among RWs (Lang et al., 2021; Muñoz et al., 2020). This is because arable farming practices were first introduced in Southeast Europe during the Neolithic period and then later spread across Eurasia (Pyšek et al., 2005). Along with agricultural practices and crop seeds, southern non-crop species associated with recurring soil disturbances also spread and established themselves in ploughed areas (Lang et al., 2021). As these species are adapted to warm climates, we observed a spatial gradient in their occurrences within the study area. Accordingly, species richness of old-field and grassland RWs were higher in the southern regions. Similar patterns were observed in studies focusing on secondary succession on former croplands in the Czech Republic, where weed diversity was higher in warmer areas (Lososová et al., 2004; Prach et al., 2014).

4.2. Percentage of arable land in the neighbouring landscape

Although previous studies reported that landscape composition, especially the proportion of arable land, influences the occurrence of RWs (Kovács-Hostyánszki et al., 2013; Rotchés-Ribalta et al., 2015b), we did not observe this pattern in our study system. A probable reason could

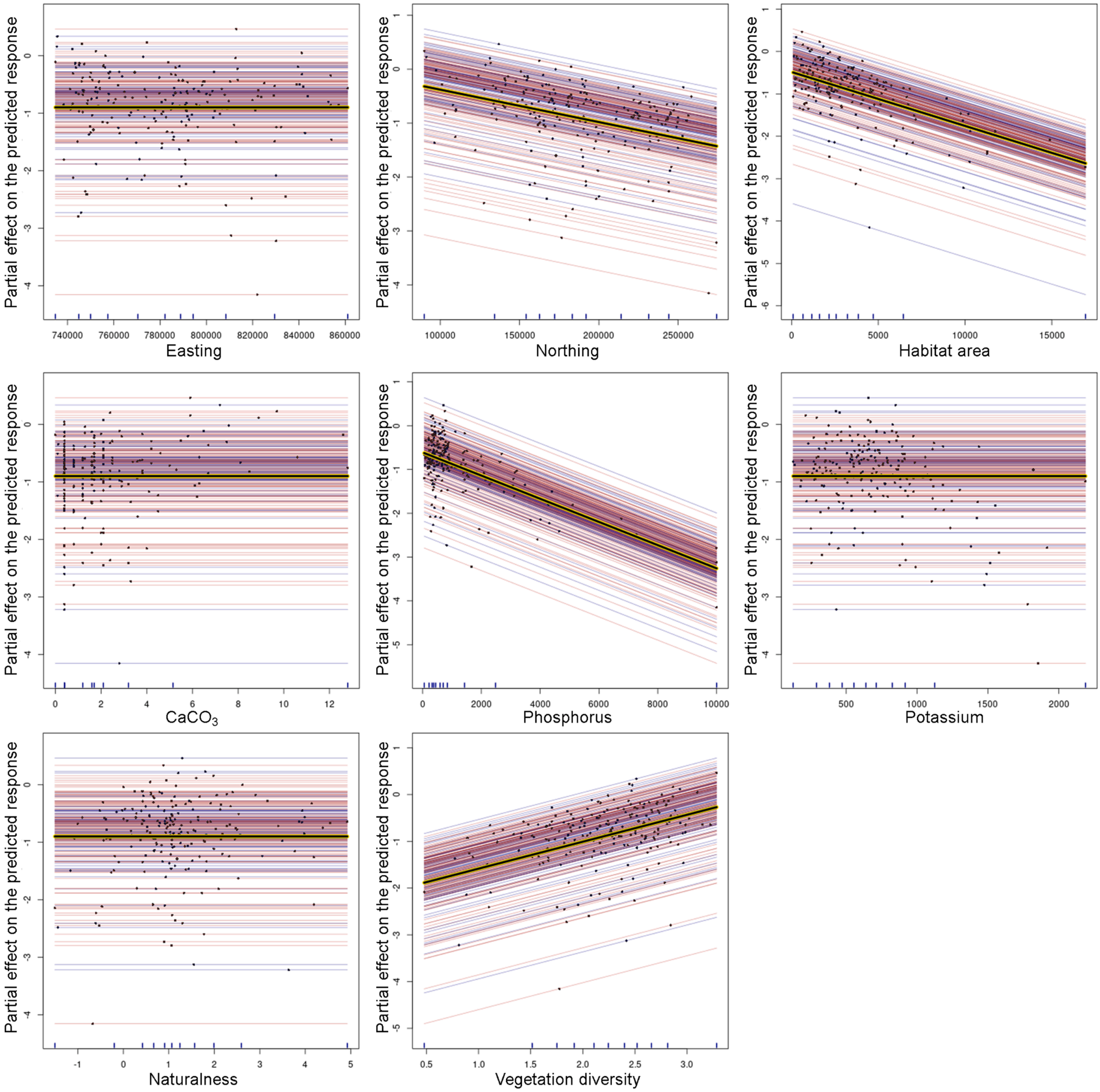


Fig. 5. Individual conditional expectation curves illustrating the effects of factors retained in zero-inflated GLMMs, selected through forward factor selection, calculated for grassland-related rare weeds. Notations: red lines – curves calculated for sites without rare weeds; blue lines – curves calculated for sites holding ≥1 rare weed species; bold black line with a yellow highlight – partial dependence plot, mean of the individual conditional expectation curves.

be that extensive arable management has almost completely disappeared from the study region during the past decades (Pinke, 2020). Consequently, our study sites were mostly surrounded by intensively managed parcels. As was highlighted by Rotchés-Ribalta et al., (2015b) the lack of an effect from arable land size may be due to that RW species might respond more strongly to local habitat conditions than to landscape characteristics. For all three RW ecological groups, dispersal limitations caused by large homogenous croplands surrounding the small grassland fragments may have been mitigated by seed dispersal via agricultural machinery that are generally used in various habitat types present in the landscape (Chaudron and Isselin-Nondedeu, 2017). Besides the proportion of arable land, the cultivated crop type may also influence RW species richness and composition of rare arable weed flora in successional grasslands (Fried et al., 2008; Pinke et al., 2012). However, unfortunately, due to the large number of sites (many of which were old-fields over 20 years), we could not compile a comprehensive dataset on former cultivated crop types, however it can be established that crop rotation was typical around most of our study sites.

4.3. Habitat area

Based on the island biogeography theory (MacArthur and Wilson, 1967), it can be assumed that larger terrestrial islands harbour more species. However, we found a negative species-area relationship for RW

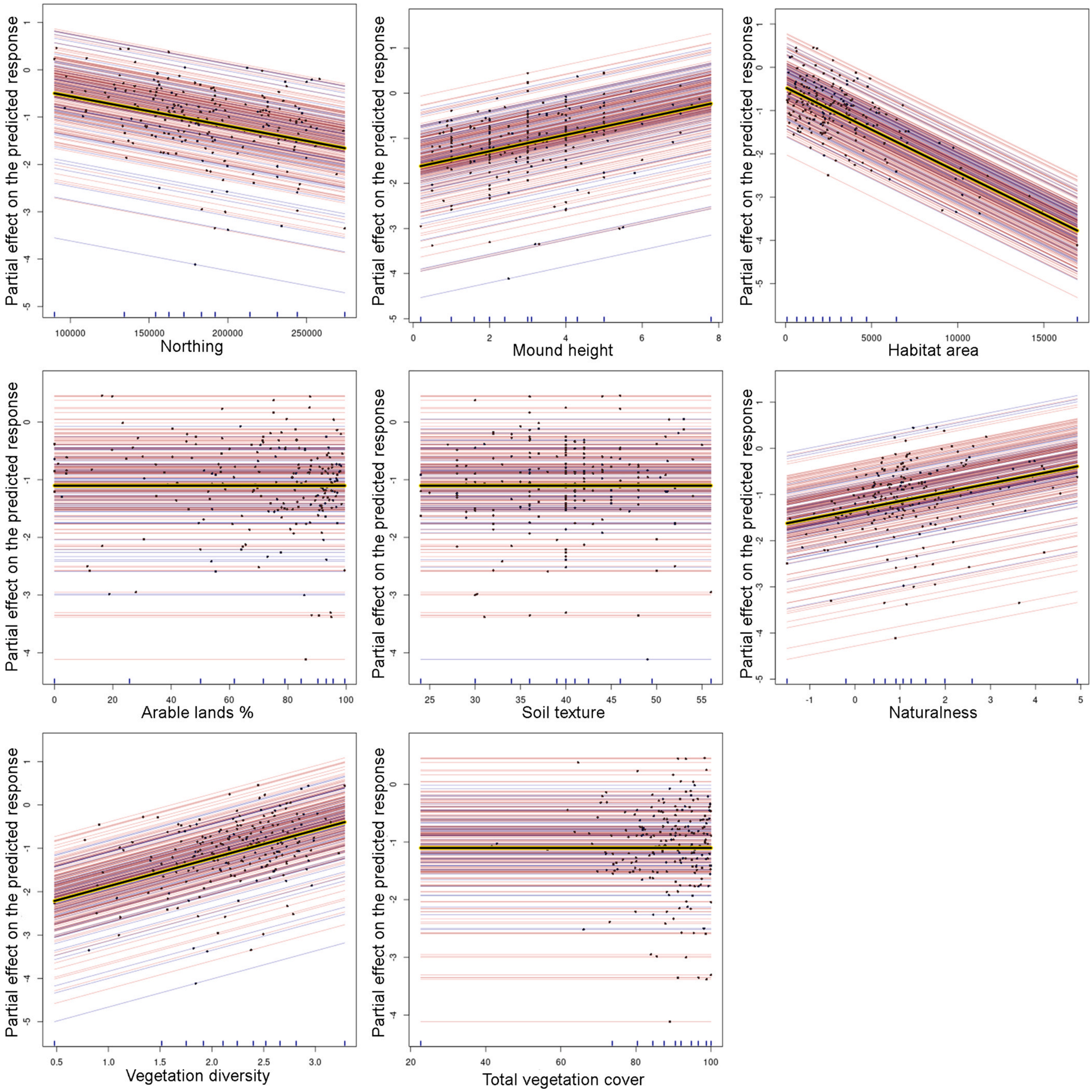


Fig. 6. Individual conditional expectation curves illustrating the effects of factors retained in zero-inflated GLMMs, selected through forward factor selection, calculated for old-field-related rare weeds. Notations: red lines – curves calculated for sites without rare weeds; blue lines – curves calculated for sites holding ≥1 rare weed species; bold black line with a yellow highlight – partial dependence plot, mean of the individual conditional expectation curves.

species. This negative effect of habitat area on old-field and grassland RW species numbers might be due to that smaller out-of-production sites typically have a larger perimeter to core area ratio. Although the sites in this study were not subjected to any agricultural management after ploughing was ceased, they might still be influenced by side effects of agricultural activities (e.g., low intensity soil disturbance that can maintain an open vegetation structure) near their borders where out-of-production sites contact with neighbouring croplands. Despite their patch-like shape, smaller sites, may have similar functions as linear field margins and road verges characterised by large perimeter to core area ratio, which are known to serve as important safe havens for grassland and old-field RW species (Brückmann et al., 2010; Deák et al., 2021b). The reduced number of old-field and grassland RW species in larger sites might be explained by the presence of closed vegetation composed by the established grassland species due to the large core areas where disturbance level is lower.

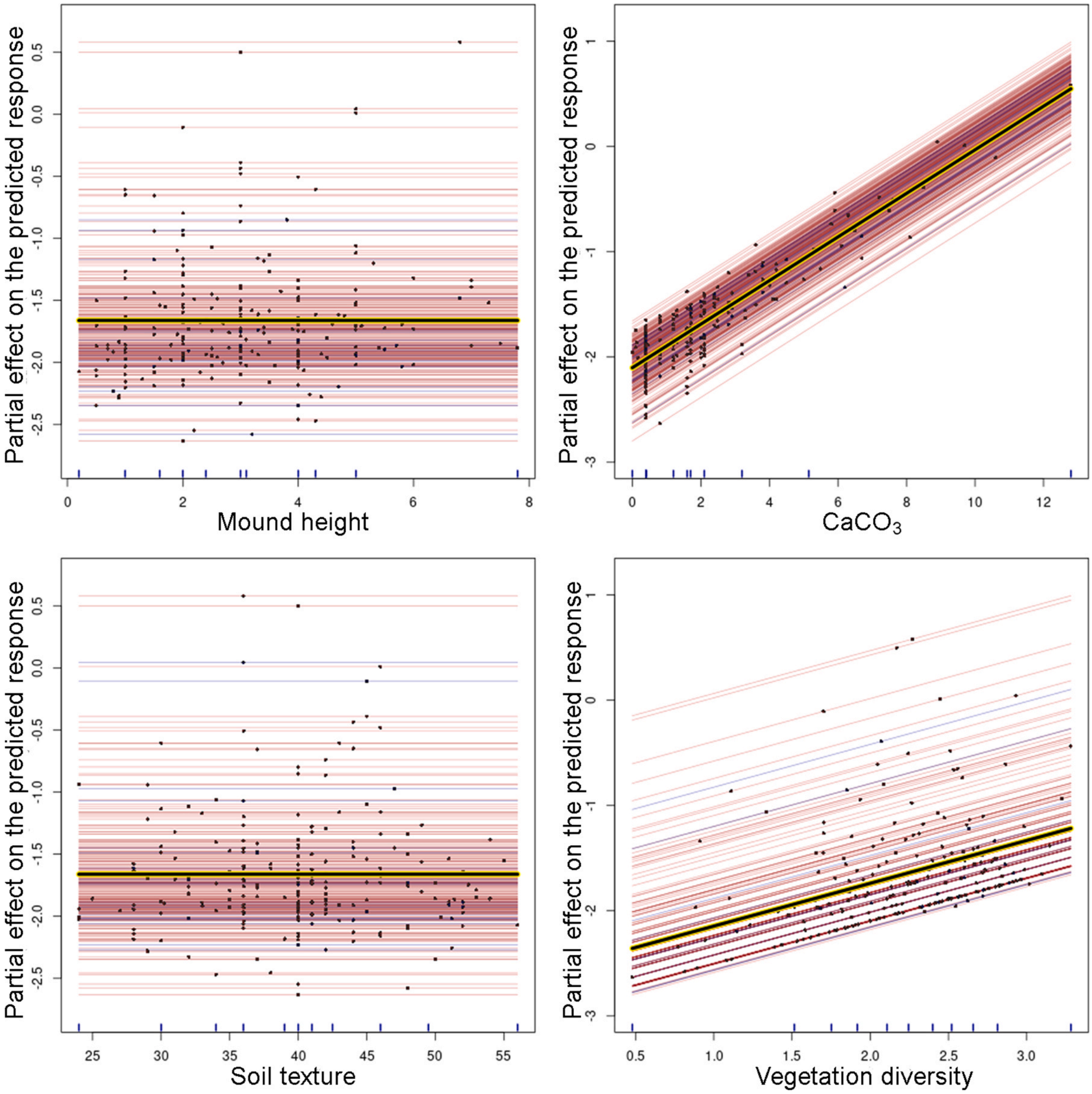


Fig. 7. Individual conditional expectation curves illustrating the effects of factors retained in zero-inflated GLMMs, selected through forward factor selection, calculated for arable rare weeds. Notations: red lines – curves calculated for sites without rare weeds; blue lines – curves calculated for sites holding ≥1 rare weed species; bold black line with a yellow highlight – partial dependence plot, mean of the individual conditional expectation curves.

4.4. Environmental heterogeneity

We found that increased environmental heterogeneity (expressed by the relative height of the mound) significantly influenced both the occurrence possibility and species richness of RWs. Due to differences in solar radiation, slopes with different aspects hold distinct microclimates on mounds (Deák et al., 2021b). Relative to the surrounding flat landscape, the north-facing slopes hold constantly mild, the south-facing slopes and the top of the mound hold constantly stressed conditions regarding air temperature, relative humidity and soil moisture. Due to the daily changes in the amount of solar radiation received by the east- and west-facing slopes, they hold dynamically fluctuating stressed and mild conditions, respectively (Deák et al., 2021b). Differences between microsites increase with increasing mound height, allowing higher mounds to provide more diverse niches for RW species. This heterogeneity enhanced the establishment of arable RW species, as larger variety of niches could support more species from the landscape level species pool to be established (Stein et al., 2014). Similarly, species richness of old-field RWs adapted to conditions in both croplands and grasslands benefited from the environmental heterogeneity of high kurgans.

4.5. Soil properties

Pinke and Gunton (2014) found that the effect of nutrient surplus on arable RWs might last longer than the other effects of agricultural cultivation, such as tillage and herbicides. However, we found that among the three studied nutrients (N, P, and K), only phosphorus affected RWs. On soils with higher phosphorus content, the species richness of grassland RWs was lower. As Rotchés-Ribalta et al. (2020) found, fertilisation does not significantly affect most arable RW species when grown alone, but when grown alongside crops it stimulates crop growth leading to the suppression of RWs. A similar mechanism may operate in grassland RWs in our study system, where higher phosphorus levels support the development of a closed successional vegetation, intensifying competition and closing habitat gaps.

Our results showed that grassland RW species typical of disturbed, but basically nutrient-poor habitats are especially sensitive to increased phosphorus concentrations. Increased phosphorus levels can indirectly suppress RWs by supporting biomass production and therefore increasing competition for light, and decreasing the availability of open gaps (Storkey et al., 2012). Phosphorus may have stronger effects than nitrogen because nitrogen diminishes rapidly through plant uptake, leaching, mineralisation, denitrification, and volatilization from the soil of formerly fertilised arable lands, while due to the strong binding to soil particles, chemical fixation and low solubility phosphorus is less mobile (Alt et al., 2011).

Although we expected that RWs can be established more successfully on poor, sandy soils due to less intense management and slightly different species pool of RWs in such areas (Fried et al., 2008; Pinke et al., 2012), this effect was weak (shown by the marginally significant positive estimate in the zero-inflated model) likely because differences in soil properties were marginal.

We found that high $CaCO_3$ content of the soil resulted in a high species richness of arable RWs. This is in line with the results of former studies that showed that weed communities considerably differ on acidic and basic bedrock (Fried et al., 2008; Pinke et al., 2012, 2024; Prach et al., 2014). In general, species richness of Central-European dry grasslands is higher on soil with higher $CaCO_3$ content (Chytrý et al., 2003) which can be a reason for the higher number of arable RWs in our study on more basic soil.

4.6. Age and characteristics of vegetation

Although our dataset covered a long chronosequence of successional grasslands, we observed that only the diversity of the recovering vegetation had any effect on RWs. Previous studies from Central and Western Europe reported that early successional stages of abandoned, uncultivated parcels are generally dominated by diverse annual weed communities (Lososová et al., 2004; Sojneková and Chytrý, 2015). Over time, annual weed species are replaced by annual and perennial grassland species in cases when their propagules are present in the surrounding landscape (Sojneková and Chytrý, 2015). In the case of arable RWs, studies by Lososová et al. (2004), and Prach et al. (2014) confirmed this pattern, reporting a decline in arable RWs over time in passively regenerating grasslands in the Czech Republic. Similarly, in their study involving 158 set-asides in East Germany, Waldhardt (1994) found that most of the red-listed annual RWs were present in two-year-old fallows. Accordingly, we assumed that arable RWs typically peak in young fallows, and decline as succession progresses, while the species richness of annual grassland-related RWs increases in later successional phases. The mechanism underlying this pattern is that, during grassland succession, arable RWs can be suppressed by the lack of recurring soil disturbances related to arable farming. Such disturbances are necessary to prevent the formation of a dense vegetation by competitive species, and the accumulation of a thick litter layer both inhibiting the establishment of RWs from the seed rain and seed bank (Albrecht, 2004; Ruprecht and Szabó, 2012). Since most RWs are annual, their persistence especially depends on factors that provide suitable conditions for successful seedling emergence (Muñoz et al., 2020). In our study system, the burrowing activities of small mammals might have counteracted these inhibitory effects by maintaining open soil gaps. This phenomenon was described by previous studies (Godó et al., 2018, 2025), demonstrating that red foxes (*Vulpes vulpes* L.) and steppe mice (*Mus spicilegus* Petényi) can create and maintain a temporarily stable network of establishment gaps in successional grasslands embedded in agroecosystems. The presence of these establishment gaps may explain the lack of a significant effect of age and total vegetation cover on RWs. Since our data represented entire sites, small open patches were not captured in total vegetation cover scores, potentially obscuring their contribution to RW dynamics.

Sites holding diverse vegetation supported significantly higher species richness of RWs that were obligatorily (grassland RWs) or facultatively (old-field RWs) associated with grasslands. This finding suggests that these species prefer vegetation with an even distribution of many species rather than vegetation dominated by a few strong competitor species (such as *Festuca* spp. which are typical of dry grasslands in the region). However, the naturalness of the vegetation that positively correlated with age, did not significantly affect RWs, suggesting that grassland-related RWs do not require fully recovered grassland vegetation. This highlights the importance of grasslands in diverse successional stages for the conservation of RWs.

5. Outlook and conservation remarks

Our study demonstrated that, in agricultural landscapes, out-of-production sites can provide safe havens for RW species associated with arable lands, old-fields, and grasslands. These sites can contribute to RW conservation by providing a unique combination of co-occurring microhabitats. This includes a central, patch-like habitat covered with spontaneously recovering vegetation, together with the non-cultivated field margins and less intensively managed crop edges at the border zone of arable parcels and out-of-production sites. Although in the present study we did not investigate the species pool of edges, previous studies indicate that they generally hold more arable RWs than central parts of parcels, because management intensity decreases from the central parts towards the edges (Fried et al., 2009; Pinke et al., 2012; Rotchés-Ribalta et al., 2020). Compared to the centre of the parcels, the levels of soil cultivation, crop densities, fertilisation and the amounts of pesticides and herbicides applied are lower at the edges (Kleijn and van der Voort, 1997; Rotchés-Ribalta et al., 2020; Storkey et al., 2012). According to José-María et al. (2010) this difference in management intensity can be up to 55 %. Consequently, crop yield and competition by crops are considerably lower at crop edges, supporting the establishment of arable and old-field RW species (Pinke et al., 2014; Nowak et al., 2019).

Even covered with ruderal vegetation, the margins of out-of-production sites can provide habitat for all RW groups, and these marginal habitats can also contribute to the landscape-scale habitat diversity. The core area of larger out-of-production sites might provide suitable habitats primarily to grassland-related RWs in case the vegetation does not form a closed structure. Since the crop edge, field margin and core areas have the potential for dynamic species exchange (Gaba et al., 2010; Muñoz et al., 2020; Pinke et al., 2012; Rotchés-Ribalta et al., 2015a), their combined effect is larger than the individual effect of each habitat type. The co-existence of these habitat types can buffer the stochastic events (such as spraying chemicals in the edge, or ploughing the field margin) affecting a certain part of the complex, as species can re-establish from the habitats remained intact.

Our results suggest that agri-environmental schemes supporting land sparing by designating out-of-production sites within agricultural landscapes can effectively promote RW conservation in general. More importantly, such schemes provide a feasible solution for protecting grassland-related RW species, which despite being included in red lists, are often overlooked in RW conservation efforts.

CRediT authorship contribution statement

Orsolya Valkó: Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Laura Godó:** Writing – review & editing, Visualization, Investigation. **Csaba Tölgyesi:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Kristóf Süveges:** Writing – review & editing, Methodology, Investigation, Data curation, Conceptualization. **Ákos Bede-Fazekas:** Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Balázs Deák:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **András Kelemen:** Investigation. **Sándor Borza:** Investigation. **Ádám Bede:** Investigation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix

Appendix Table 1
List and attributes of environmental and land use factors considered in the study, with an indication for those which were included in the final model.

Factor	Used in the final model	Unit	Range	Mean	SD
Northing	yes	m	89926.28 – 274225.20	186340.81	41542.22
Easting	yes	m	734746.32 – 861067.57	782029.56	31362.41
Percentage of arable land in the neighbouring landscape	yes	%	0.00 – 99.48	70.00	27.12
Percentage of grassland in the neighbouring landscape	no	%	0.00 – 89.79	13.17	19.95
Distance to the nearest grassland	no	m	0.00 – 4068.00	202.11	429.12
Hanski connectivity index	no	-	0.00 – 865.83	155.52	171.17
Habitat area	yes	m^2	90.00 – 16942.00	3258.63	2773.98
Mound height	yes	m	0.20 – 7.80	3.01	1.60
Soil nitrogen content	yes	mg/kg	0.28 – 102.47	10.92	13.62
Soil phosphorus content	yes	mg/kg	58.10 – 10000.00	1088.88	1537.77
Soil potassium content	yes	mg/kg	127.00 – 2188.00	695.01	362.92
Soil texture	yes	-	24.00 – 56.00	39.74	7.00
Soil $CaCO_3$ content	yes	m/m %	0.00 – 12.80	2.13	2.25
Age	yes	year	0.00 – 3.70	1.33	0.92
Total vegetation cover	yes	%	22.70 – 100.00	87.72	11.03
Shannon diversity of vegetation	yes	-	0.48 – 3.28	2.19	0.53
Naturalness of the vegetation	yes	-	-1.50 – 4.92	1.22	1.17

Appendix Table 2
List, functional group, frequency, distribution range, and protection status of rare weed species on the studied out-of-production sites (n = 216).

Species name	RW group	Frequency proportion in the studied quadrats (%)	Frequency in the studied sites (number of occurrences)	Distribution area	IUCN	Hungarian Red list	National protection in Hungary
Acinos arvensis	grassland	**19.4**	1	European	-	-	-
Adonis flammea	arable	**2.2**	2	Pontic-Submediterranean	-	Near threatened	-
Aegilops cylindrica	grassland	**22.4**	17	Eurasian	Least concern	Near threatened	-
Ajuga chamaepytis	old-field	**19.9**	9	Submediterranean	-	-	-
Alcea biennis	grassland	**2.9**	1	Pontic-Submediterranean	-	-	-
Allium atropurpureum	grassland	**14.5**	1	Pannon-Balkan	-	Near threatened	-
Althaea hirsuta	old-field	**1.5**	1	Pontic-Submediterranean	-	Near threatened	-
Androsace elongata	old-field	**5.1**	5	Pontic	-	-	-
Calepina irregularis	old-field	**5.2**	5	Mediterranean	-	-	-
Caucalis platycarpos	old-field	**8.4**	3	Submediterranean	-	-	-
Centaurea cyanus	arable	**8.8**	5	Cosmopolitan	-	-	-
Centaurea solstitialis	grassland	**12.5**	1	Eurasian	-	Near threatened	-
Cynoglossum hungaricum	grassland	**1.3**	1	Pannon-Balkan	Data deficient	-	-
Erigeron acris	grassland	**18.4**	1	Circumpolar	-	-	-
Erodium ciconium	grassland	**1.9**	3	Adventive	-	Near threatened	-
Filago arvensis	grassland	**2.9**	4	Submediterranean	-	-	-
Filago vulgaris	old-field	**0.2**	3	Eurasian	-	Near threatened	-
Geranium dissectum	old-field	**13.6**	16	Eurasian	-	-	-
Glaucium corniculatum	old-field	**0.8**	2	Submediterranean	-	-	-
Lathyrus hirsutus	old-field	**15.8**	8	Eastern-Submediterranean	Least concern	-	-
Lathyrus nissolia	old-field	**13.1**	4	(Sub)atlantic-submediterranean	-	-	Protected
Lycopsis arvensis	arable	**2.2**	7	European	Vulnerable	Near threatened	-
Medicago monspeliaca	grassland	**1.2**	3	Submediterranean	-	Near threatened	-
Nigella arvensis	arable	**11.3**	3	Pontic-Submediterranean	-	-	-
Papaver hybridum	arable	**2.5**	4	Submediterranean	Vulnerable	Near threatened	-
Ranunculus arvensis	arable	**20.2**	2	Eurasian	-	-	-
Rapistrum perenne	grassland	**1.2**	1	Pontic-Submediterranean	-	-	-
Reseda inodora	grassland	**0.2**	2	Pontic-Pannonic	-	Endangered	Protected
Reseda luteola	old-field	**0.7**	1	Eurasian	-	-	-
Sherardia arvensis	arable	**1.3**	1	Cosmopolitan	-	-	-
Sideritis montana	old-field	**1.3**	2	Eurasian	-	-	-
Sisymbrium altissimum	grassland	**21.9**	1	Eurasian	-	-	-
Sisymbrium orientale	old-field	**22.6**	3	Pontic-Submediterranean	-	-	-
Thesium linophyllum	old-field	**6.1**	1	Central-European	-	-	-
Trifolium diffusum	grassland	**3.2**	8	Pontic-Submediterranean	-	Near threatened	-
Trigonella procumbens	grassland	**2.7**	2	Pontic-Submediterranean	-	Near threatened	-
Ventenata dubia	grassland	**5.2**	13	Submediterranean	Least concern	-	-
Vulpia myuros	grassland	**5.4**	31	Cosmopolitan	-	-	-

Appendix Table 3

Correlations between the studied factors (Pearson's correlation coefficients and significances).

	Pearson's correlation coefficients																
	Easting	Northing	Age	Mound height	Habitat area	Arable %	Grassland %	Nearest grassland distance	Hanski index	Soil CaCO3 content	Soil texture	Soil P content	Soil K content	Soil N content	Naturalness of the vegetation	Shannon diversity of vegetation	Total vegetation cover
Easting	1.0	0.5	0.2	-0.1	-0.1	0.0	0.0	0.0	0.0	-0.2	0.2	0.0	0.0	0.2	0.0	0.0	0.1
Northing	0.5	1.0	0.0	0.1	0.2	-0.1	0.1	-0.1	0.1	-0.4	-0.1	-0.1	-0.1	0.0	0.1	0.2	0.1
Age	0.2	0.0	1.0	0.4	-0.1	-0.1	-0.1	0.2	0.0	0.1	0.2	-0.1	0.0	0.4	0.3	-0.1	0.2
Mound height	-0.1	0.1	0.4	1.0	0.2	0.1	-0.3	0.1	-0.2	0.1	-0.1	0.0	-0.1	0.2	0.0	0.1	0.1
Habitat area	-0.1	0.2	-0.1	0.2	1.0	0.1	0.0	0.1	0.1	-0.1	0.0	0.1	0.1	-0.1	0.0	0.1	0.0
Arable %	0.0	-0.1	-0.1	0.1	0.1	1.0	-0.8	0.3	-0.8	0.1	-0.2	0.0	-0.1	0.0	-0.3	-0.1	-0.1
Grassland %	0.0	0.1	-0.1	-0.3	0.0	-0.8	1.0	-0.3	0.9	-0.1	0.2	-0.1	0.1	0.0	0.4	0.1	0.1
Nearest grassland distance	0.0	-0.1	0.2	0.1	0.1	0.3	-0.3	1.0	-0.4	0.2	0.0	0.0	0.1	0.1	0.0	-0.1	0.0
Hanski index	0.0	0.1	0.0	-0.2	0.1	-0.8	0.9	-0.4	1.0	-0.1	0.2	0.0	0.1	-0.1	0.3	0.1	0.1
Soil $CaCO_3$ content	-0.2	-0.4	0.1	0.1	-0.1	0.1	-0.1	0.2	-0.1	1.0	0.0	0.0	-0.1	0.0	0.0	-0.1	0.0
Soil texture	0.2	-0.1	0.2	-0.1	0.0	-0.2	0.2	0.0	0.2	0.0	1.0	0.1	0.5	0.2	0.1	0.0	0.2
Soil P content	0.0	-0.1	-0.1	0.0	0.1	0.0	-0.1	0.0	0.0	0.0	0.1	1.0	0.5	0.1	-0.2	-0.1	0.0
Soil K content	0.0	-0.1	0.0	-0.1	0.1	-0.1	0.1	0.1	0.1	-0.1	0.5	0.5	1.0	0.1	-0.2	0.0	0.1
Soil N content	0.2	0.0	0.4	0.2	-0.1	0.0	0.0	0.1	-0.1	0.0	0.2	0.1	0.1	1.0	0.1	-0.1	0.1
Naturalness of the vegetation	0.0	0.1	0.3	0.0	0.0	-0.3	0.4	0.0	0.3	0.0	0.1	-0.2	-0.2	0.1	1.0	0.0	0.0
Shannon diversity of vegetation	0.0	0.2	-0.1	0.1	0.1	-0.1	0.1	-0.1	0.1	-0.1	0.0	-0.1	0.0	-0.1	0.0	1.0	-0.1
Total vegetation cover	0.1	0.1	0.2	0.1	0.0	-0.1	0.1	0.0	0.1	0.0	0.2	0.0	0.1	0.1	0.0	-0.1	1.0

	Significances																
	Easting	Northing	Age	Mound height	Habitat area	Arable %	Grassland %	Nearest grassland distance	Hanski index	Soil CaCO3 content	Soil texture	Soil P content	Soil K content	Soil N content	Naturalness of the vegetation	Shannon diversity of vegetation	Total vegetation cover
Easting	NA	0.000	0.003	0.307	0.110	0.723	0.629	0.932	0.808	0.001	0.015	0.937	0.656	0.001	1.000	0.554	0.357
Northing	0.000	NA	0.497	0.210	0.001	0.178	0.389	0.259	0.057	0.000	0.197	0.173	0.390	0.511	0.200	0.002	0.089
Age	0.003	0.497	NA	0.000	0.044	0.340	0.420	0.027	0.769	0.268	0.007	0.145	0.628	0.000	0.000	0.310	0.003
Mound height	0.307	0.210	0.000	NA	0.007	0.032	0.000	0.076	0.011	0.305	0.249	0.867	0.038	0.003	0.877	0.050	0.112
Habitat area	0.110	0.001	0.044	0.007	NA	0.287	0.993	0.318	0.372	0.071	0.862	0.395	0.297	0.056	0.906	0.344	0.966
Arable %	0.723	0.178	0.340	0.032	0.287	NA	0.000	0.000	0.000	0.186	0.005	0.995	0.147	0.643	0.000	0.453	0.073
Grassland %	0.617	0.652	0.999	0.006	0.964	0.000	0.000	0.340	0.000	0.616	0.263	0.405	0.258	0.920	0.000	0.948	0.770
Nearest grassland distance	0.629	0.389	0.420	0.000	0.993	0.000	NA	0.000	0.000	0.108	0.001	0.357	0.060	0.606	0.000	0.350	0.211
Hanski index	0.932	0.259	0.027	0.076	0.318	0.000	0.000	NA	0.000	0.024	0.860	0.673	0.253	0.223	0.531	0.442	0.645
Soil $CaCO_3$ content	0.808	0.057	0.769	0.011	0.372	0.000	0.000	0.000	NA	0.034	0.004	0.668	0.042	0.384	0.000	0.051	0.203
Soil texture	0.001	0.000	0.268	0.305	0.071	0.186	0.108	0.024	0.034	NA	0.975	0.598	0.172	0.743	0.796	0.339	0.827
Soil P content	0.015	0.197	0.007	0.249	0.862	0.005	0.001	0.860	0.004	0.975	NA	0.198	0.000	0.000	0.214	0.912	0.016
Soil K content	0.937	0.173	0.145	0.867	0.395	0.995	0.357	0.673	0.668	0.598	0.198	NA	0.000	0.299	0.000	0.345	0.746
Soil N content	0.656	0.390	0.628	0.038	0.297	0.147	0.060	0.253	0.042	0.172	0.000	0.000	NA	0.161	0.021	0.556	0.276
Naturalness of the vegetation	0.001	0.511	0.000	0.003	0.056	0.643	0.606	0.223	0.384	0.743	0.000	0.299	0.161	NA	0.429	0.061	0.244
Shannon diversity of vegetation	1.000	0.200	0.000	0.877	0.906	0.000	0.000	0.531	0.000	0.796	0.214	0.000	0.021	0.429	NA	0.809	0.790
Total vegetation cover	0.554	0.002	0.310	0.050	0.344	0.453	0.350	0.442	0.051	0.339	0.912	0.345	0.556	0.061	0.809	NA	0.248
OB_total_veg_cover	0.357	0.089	0.003	0.112	0.966	0.073	0.211	0.645	0.203	0.827	0.016	0.746	0.276	0.244	0.790	0.248	NA

Appendix Table 4

Correlations between the studied factors (Spearman's correlation coefficients and significances).

	Spearman's correlation coefficients																
	Easting	Northing	Age	Mound height	Habitat area	Arable %	Grassland %	Nearest grassland distance	Hanski index	Soil CaCO3 content	Soil texture	Soil P content	Soil K content	Soil N content	Naturalness of the vegetation	Shannon diversity of vegetation	Total vegetation cover
Easting	1.0	0.5	0.1	-0.1	-0.1	0.0	0.0	0.0	0.0	-0.2	0.2	0.0	0.0	0.0	0.0	0.1	0.2
Northing	0.5	1.0	0.1	0.1	0.2	-0.1	0.1	-0.1	0.1	-0.3	-0.1	-0.2	-0.1	0.0	0.2	0.2	0.2
Age	0.1	0.1	1.0	0.2	-0.1	-0.2	0.1	-0.2	0.2	0.0	0.2	-0.1	0.1	0.4	0.4	0.0	0.4
Kurgan height	-0.1	0.1	0.2	1.0	0.3	0.1	-0.2	0.1	-0.2	0.0	-0.1	-0.1	-0.2	0.2	0.0	0.2	0.0
Kurgan area	-0.1	0.2	-0.1	0.3	1.0	0.1	0.0	0.0	0.0	-0.1	0.0	0.0	0.0	-0.1	0.0	0.2	-0.2
Arable %	0.0	-0.1	-0.2	0.1	0.1	1.0	-0.8	0.6	-0.8	0.1	-0.2	0.1	-0.1	-0.1	-0.2	-0.1	-0.1
Grassland %	0.0	0.1	0.1	-0.2	0.0	-0.8	1.0	-0.7	1.0	-0.1	0.2	-0.1	0.2	0.0	0.2	0.1	0.0
Nearest grassland distance	0.0	-0.1	-0.2	0.1	0.0	0.6	-0.7	1.0	-0.8	0.2	-0.2	0.2	-0.1	0.1	-0.3	-0.1	-0.1
Hanski index	0.0	0.1	0.2	-0.2	0.0	-0.8	1.0	-0.8	1.0	-0.2	0.2	-0.1	0.2	-0.1	0.3	0.2	0.0
Soil CaCO3 content	-0.2	-0.3	0.0	0.0	-0.1	0.1	-0.1	0.2	-0.2	1.0	-0.1	0.1	-0.1	0.1	-0.1	-0.1	0.0
Soil texture	0.2	-0.1	0.2	-0.1	0.0	-0.2	0.2	-0.2	0.2	-0.1	1.0	0.2	0.5	0.2	0.0	0.0	0.1
Soil P content	0.0	-0.2	-0.1	-0.1	0.0	0.1	-0.1	0.2	-0.1	0.1	0.2	1.0	0.5	0.1	-0.3	-0.1	0.0
Soil K content	0.0	-0.1	0.1	-0.2	0.0	-0.1	0.2	-0.1	0.2	-0.1	0.5	0.5	1.0	0.2	-0.1	0.0	0.0
Soil N content	0.0	0.0	0.4	0.2	-0.1	-0.1	0.0	0.1	-0.1	0.1	0.2	0.1	0.2	1.0	0.0	-0.1	0.1
Naturalness of the vegetation	0.0	0.2	0.4	0.0	0.0	-0.2	0.2	-0.3	0.3	-0.1	0.0	-0.3	-0.1	0.0	1.0	0.1	0.0
Shannon diversity of vegetation	0.1	0.2	0.0	0.2	0.2	-0.1	0.1	-0.1	0.2	-0.1	0.0	-0.1	0.0	-0.1	0.1	1.0	-0.1
Total vegetation cover	0.2	0.2	0.4	0.0	-0.2	-0.1	0.0	-0.1	0.0	0.0	0.1	0.0	0.0	0.1	0.0	-0.1	1.0

	Significances																
	Easting	Northing	Age	Kurgan height	Kurgan area	Arable %	Grassland %	Nearest grassland distance	Hanski index	Soil CaCO3 content	Soil texture	Soil P content	Soil K content	Soil N content	Naturalness of the vegetation	Shannon diversity of vegetation	Total vegetation cover
Easting	NA	0	0.358	0.111	0.110	0.884	0.750	0.831	0.776	0.005	0.001	0.728	0.828	0.849	0.580	0.389	0.016
Northing	0	NA	0.210	0.153	0.001	0.157	0.388	0.044	0.136	0.000	0.322	0.001	0.136	0.737	0.015	0.002	0.014
Age	0.358	0.210	NA	0.003	0.044	0.002	0.029	0.001	0.021	0.729	0.002	0.347	0.313	0.000	0.000	0.984	0.000
Mound height	0.111	0.153	0.003	NA	0.000	0.124	0.003	0.081	0.011	0.757	0.059	0.434	0.012	0.007	0.916	0.007	0.500
Habitat area	0.110	0.001	0.044	0.000	NA	0.262	0.620	0.484	0.987	0.048	0.520	0.839	0.572	0.030	0.989	0.010	0.010
Arable %	0.884	0.157	0.002	0.124	0.262	NA	0.000	0.000	0.000	0.046	0.006	0.171	0.420	0.358	0.001	0.207	0.366
Grassland %	0.750	0.388	0.029	0.003	0.620	0.000	NA	0.000	0.000	0.028	0.001	0.337	0.022	0.600	0.000	0.029	0.967
Nearest grassland distance	0.831	0.044	0.001	0.081	0.484	0.000	0.000	NA	0.000	0.001	0.012	0.017	0.224	0.422	0.000	0.194	0.250
Hanski index	0.776	0.136	0.021	0.011	0.987	0.000	0.000	0.000	NA	0.007	0.001	0.229	0.027	0.410	0.000	0.023	0.881
Soil CaCO$_3$ content	0.005	0.000	0.729	0.757	0.048	0.046	0.028	0.001	0.007	NA	0.459	0.104	0.051	0.322	0.105	0.076	0.869
Soil texture	0.001	0.322	0.002	0.059	0.520	0.006	0.001	0.012	0.001	0.459	NA	0.008	0.000	0.008	0.585	0.982	0.045
Soil P content	0.728	0.001	0.347	0.434	0.839	0.171	0.337	0.017	0.229	0.104	0.008	NA	0.000	0.124	0.000	0.258	0.898
Soil K content	0.828	0.136	0.313	0.012	0.572	0.420	0.022	0.224	0.027	0.051	0.000	0.000	NA	0.026	0.032	0.622	0.732
Soil N content	0.849	0.737	0.000	0.007	0.030	0.358	0.600	0.422	0.410	0.322	0.008	0.124	0.026	NA	0.516	0.043	0.044
Naturalness of the vegetation	0.389	0.002	0.984	0.007	0.010	0.207	0.029	0.194	0.023	0.076	0.982	0.258	0.622	0.043	0.246	NA	0.068
Shannon diversity of vegetation	0.568	0.732	0.000	0.055	0.778	0.000	0.000	0.000	0.000	0.246	0.000	0.967	0.010	0.226	0.000	0.697	0.126
Total vegetation cover	0.016	0.014	0.000	0.500	0.010	0.366	0.967	0.250	0.881	0.869	0.045	0.898	0.732	0.044	0.467	0.068	NA

Appendix Table 5
Multicollinearity among the studied variables.

Factor	GVIF
Northing	1.991
Easting	1.738
Percentage of arable land	1.266
Kurgan area	1.265
Mound height	1.452
Soil nitrogen content	1.415
Soil phosphorus content	1.511
Soil potassium content	2.011
Soil texture	1.687
Soil $CaCO_3$ content	1.254
Age	2.167
Naturalness of vegetation	1.609
Shannon diversity of vegetation	1.133
Total vegetation cover	1.216

Appendix Table 6
Effects of site- and landscape-level variables on the occurrence possibility and species richness of total rare weeds, and arable land, old-field and grassland related rare weeds (zero inflated GLMMs with backward model selection; n = 216). The results of the zero inflated and poisson models are shown separately. Significant effects ($p < 0.05$) are marked with boldface.

Zero inflated models								
	Dependent variables – occurrence of rare weeds (RWs)							
	Total RW		**Arable RW**		**Old-field RW**		**Grassland RW**	
	Coefficient	Significance	Coefficient	Significance	Coefficient	Significance	Coefficient	Significance
Intercept	-425.595	1.000	0.050	0.953	-279.076	0.997	-366.598	0.360
Northing	227.310	1.000	-	-	-	-	-	-
Easting	134.729	1.000	-	-	-	-	152.127	0.359
Percentage of arable land	-	-	-	-	170.372	0.999	-	-
Habitat area	21.272	1.000	-	-	-	-	-	-
Mound height	-	-	**-2.047**	**0.036**	-	-	-	-
Soil nitrogen content	-	-	-	-	-	-	-	-
Soil phosphorus content	-	-	-	-	-	-	-	-
Soil potassium content	194.546	1.000	-	-	-	-	-160.263	0.363
Soil texture	-	-	1.340	0.061	160.289	0.998	-	-
Soil $CaCO_3$ content	-	-	-	-	-	-	90.833	0.349
Age	-	-	-	-	-	-	-	-
Naturalness of vegetation	-224.633	1.000	-	-	189.667	0.998	-256.808	0.360
Shannon diversity of vegetation	-	-	-	-	-201.227	0.998	-	-
Total vegetation cover	-54.471	1.000	-	-	-295.927	0.998	-	-
Poisson models								
	Dependent variables – species richness of rare weeds (RWs)							
	Total RW		**Arable RW**		**Old-field RW**		**Grassland RW**	
	Coefficient	Significance	Coefficient	Significance	Coefficient	Significance	Coefficient	Significance
Intercept	**-0.198**	**0.024**	**-1.662**	**0.000**	**-1.104**	**0.000**	**-0.899**	**0.000**
Northing	**-0.167**	**0.029**	-	-	**-0.261**	**0.029**	**-0.250**	**0.020**
Easting	-	-	-	-	-	-	-	-
Percentage of arable land	-	-	-	-	-	-	-	-
Kurgan area	**-0.344**	**0.003**	-	-	**-0.542**	**0.009**	**-0.353**	**0.019**
Kurgan height	**0.174**	**0.039**	-	-	**0.292**	**0.012**	-	-
Soil nitrogen content	-	-	-	-	-	-	-	-
Soil phosphorus content	-	-	-	-	-	-	**-0.407**	**0.044**
Soil potassium content	-0.061	0.543	-	-	-	-	-	-
Soil texture	-	-	-	-	-	-	-	-
Soil $CaCO_3$ content	-	-	**0.466**	**0.000**	-	-	-	-
Age	0.076	0.318	-	-	-	-	-	-
Naturalness of vegetation	-	-	-	-	0.225	0.113	-	-
Shannon diversity of vegetation	**0.345**	**0.000**	0.216	0.337	**0.344**	**0.018**	**0.306**	**0.008**
Total vegetation cover	-	-	-	-	-	-	-	-

Data availability

Data will be made available on request.

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