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Scale dependency of taxonomic and functional diversity in pristine and recovered loess steppic grasslands

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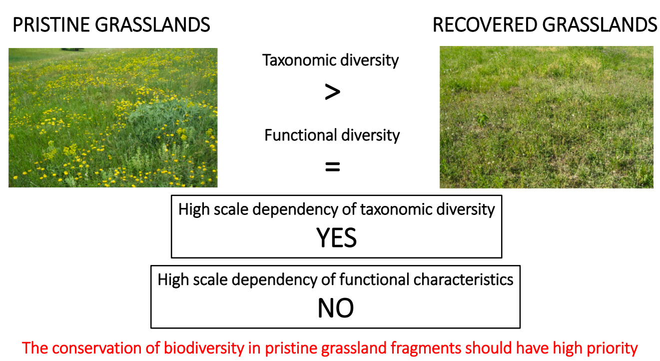
HIGHLIGHTS

- Old-growth grasslands harbour high plant biodiversity even in small patches.
- We studied the scale-dependent diversity of old-growth and secondary grasslands.
- Patterns and structure of secondary grasslands are quite like those of old-growth ones.
- The recovery of functional richness is much faster than that of taxonomic richness.
- The preservation old-growth grasslands over recovery actions should be prioritised.

GRAPHICAL ABSTRACT



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ABSTRACT

Widespread campaigns on forest restoration and various tree planting actions lower the awareness of the importance of grasslands for carbon sequestration and biodiversity conservation. Even lower attention is given to the conservation of biodiversity and ecosystem functioning in remnants of ancient, so-called pristine grasslands. Pristine grasslands generally harbour high biodiversity, and even small patches can act as important refuges for many plant and animal species in urbanised or agricultural landscapes. Spontaneous succession of grassland is frequently viewed as a cost-effective tool for grassland restoration, but its applicability is strongly dependent on many local to landscape-scale factors, and the recovery is often slow. It is therefore essential to monitor the success of grassland restoration projects that rely on spontaneous succession. We compared the species diversity and functional attributes of pristine and recovered grasslands by studying the taxonomic and functional diversity in thirteen (8 pristine and 5 recovered) loess steppic grasslands using differently sized sampling plots from 0.01 to 100 m^2. Our results indicate that there are remarkable differences in taxonomic and functional diversity

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between pristine and recovered grasslands. We also found that during secondary succession there is a likely functional saturation of the species assembly in the first few decades of recovery, and while patterns and structure of recovered grasslands became quite similar to those of pristine grasslands, species richness and diversity still remained much lower. Pristine grasslands support considerable plant diversity, and species composition is slow to recover if destroyed by agricultural land use. This underlines the importance of preserving existing pristine grassland remnants, which might serve as sources of species for future restoration measures.

1. Introduction

Grasslands are dominant landscape elements of the terrestrial land surface, covering 40 % of the land area and representing very diverse plant communities at multiple scales (White et al., 2000; Wilson et al., 2012; Dengler et al., 2014). Grasslands contribute greatly to landscape-level biodiversity and provide many ecosystem goods (e.g. feed and hay for grazing animals) and services (e.g. pollination, erosion control, water retention and filtration) (Bengtsson et al., 2019). However, there is in general a lower awareness of the importance of grasslands for carbon sequestration and biodiversity conservation compared to forests or tree plantations (Tölgyesi et al., 2022; Buisson et al., 2022). Patterns of biodiversity and ecosystem functioning in remnants of pristine grasslands receive even less attention, though understanding the relationship between biodiversity patterns and ecological processes is crucial for an effective conservation of grassland biodiversity (Török et al., 2021; Buisson et al., 2022; Silveira et al., 2022).

It has been stressed by several authors that pristine grasslands generally harbour high biodiversity and even small patches can act as important refuges for many plant and animal species in urbanised or agricultural landscapes (Dengler et al., 2014; Klaus, 2013; Lindborg et al., 2014). It has also been stressed that the small-scale biodiversity of some of these grasslands is comparable to or even larger than the biodiversity of tropical rainforests (Wilson et al., 2012). Among temperate grasslands natural dry grasslands are the most affected by anthropogenic activities and subject to severe degradation (Cousins et al., 2007; Löffler et al., 2020). The 'black' (chernozem) soil of some pristine dry grasslands like lowland steppic grasslands are highly suitable for crop production. As a result, in most countries vast areas of steppic grasslands have been destroyed and converted to arable land in the second half of the last century. In the Western part of the steppe and forest steppe zone, for example, >90 % of the former steppes have been converted to cropland or other types of intensively used farmland (Wesche et al., 2016; Deák et al., 2021a). Steppic grasslands are valuable habitats and listed as priority habitat types in the EU Habitats Directive (e.g. 6250 – Pannonic loess steppic grasslands; European Union, 1992). Former research indicated that ancient steppe grassland fragments in road verges and burial mounds can harbour high biodiversity and many plant species of conservation interest; thus, their conservation and restoration is of high priority (Sudnik-Wójcikowska et al., 2011; Deák et al., 2020a, 2020b).

Most ecological phenomena are reported to be scale-dependent, and different patterns and manifestations of their functions and biodiversity can be expected at various scales (Hewitt et al., 2017). The study of species-area relationships, starting with the pioneering works of MacArthur-Wilson on island biogeography, has been in the focus of scientific interest for decades and more recently also gained momentum in vegetation ecology (MacArthur and Wilson, 1967; Lindgren and Cousins, 2017; Ottaviani et al., 2020). Several studies have been conducted analysing the scale-dependent patterns in vegetation composition and vegetation processes, mostly focusing on relationships between biomass production, species richness and sample plot size (Palmer and White, 1994; Chiarucci et al., 2006; Dembicz et al., 2020). Compared to scale-dependent patterns in species richness, the scale dependency of some functional attributes (multi-trait functional diversity components or single-trait values) has received less attention so far (Ottaviani et al., 2020).

Spontaneous succession is frequently viewed as a cost-effective tool for grassland restoration (Prach and Hobbs, 2008), but the success of the community recovery strongly depends on the local habitat conditions and the propagule pressure from the surroundings, and the recovery process is strongly time-dependent and often slow (Ruprecht, 2006; Prach et al., 2015; Török et al., 2011a). Grassland recovery is considered to be much faster than that of forests because the development of herbaceous vegetation cover is fast and herbaceous species reach reproductive maturity earlier compared to shrubs and trees (Buisson et al., 2022). However, it has been indicated that the legacy effect of the site, for example in form of residual soil fertility or a soil seed bank of undesirable species, can hamper the regeneration process (Török et al., 2021). It has also been stressed that the community assembly of grasslands can be slow and compositional similarities between recovered and pristine grasslands remain low for several decades or even centuries (Nerlekar and Veldman, 2020; Prach et al., 2016). Well-preserved pristine grasslands are highly organised in terms of species composition and show a high degree of stability with regard to small-scale species fluctuations (Bartha et al., 2003; Virágh and Bartha, 2003; Teleki et al., 2020). Thus, for the assessment of the effectiveness of spontaneous succession as a restoration tool it is essential to compare the species diversity and functional attributes of pristine and recovered grasslands.

To analyse differences in species and functional diversity patterns and vegetation composition between recovered and pristine grasslands, we selected 13 (8 pristine and 5 recovered) grassland stands in the south-eastern part of Transdanubia, Hungary, Central Europe. We tested the following hypotheses: i) Species richness of recovered grasslands does not reach the levels found in pristine grasslands. In particular, we assumed that ia) species richness and Shannon diversity are lower, ib) the dominance of the most abundant species of the plant community is higher and ic) the functional diversity is lower in recovered grasslands than in pristine ones. We also hypothesised that ii) the difference in taxonomic and functional diversity between recovered and pristine grasslands is strongly scale-dependent. Finally, we analysed whether iii) there is a difference in species composition between recovered and pristine grasslands.

2. Materials and methods

2.1. Study region

The study region is situated in the south-eastern part of Transdanubia, Hungary, in the Tolnai-hegyhát region, near to the settlements of Szekszárd and Bonyhád (Fig. 1). The climate is moderately continental with a mean annual temperature between 10 and 11 °C and mean annual precipitation of 550–600 mm, characterised by a marked drought period in mid-summer (Mezősi, 2017).

The studied pristine grassland type is of special conservation interest and included in the Natura 2000 network as priority habitat type '6250 Pannonic loess steppic grasslands'. Loess steppic grasslands are generally characterised by a high richness of forbs and several tussock-forming or stoloniferous grasses (e.g. *Agropyron cristatum*, *Brachypodium pinnatum*, *Bromus erectus* and *B. inermis*, *Chrysopogon gryllus*, *Festuca pseudovina* and *F. rupicola* and several *Stipa* species; Illyés and Bölöni, 2007). Pristine steppic grasslands cover various types of loess deposits and were situated in naturally occurring forest-steppe openings (Borhidi et al., 2012; Erdős et al., 2018). The loess grasslands in our study region cover chernozemic soils developed on loess bedrock. Loess grasslands were historically embedded in a mosaic landscape of the forest-steppe zone (Erdős et al., 2018). The studied landscape was historically characterised by dry loess grasslands, semi-dry grasslands both with and without shrubs and fragments of open forest-steppes and closed forests (Teleki et al., 2020). Because chernozemic soils are highly suitable for agricultural production, pristine loess vegetation has only survived on road verges and on sites that are unfavourable or difficult to cultivate (e.g. steep valley sides or burial mounds; Deák et al., 2016). After the Second World War and again after the collapse of the socialist economy, several crop fields were abandoned because of insufficient funds for their cultivation. These areas became subjected to secondary succession and were reclaimed by grassland vegetation (see papers on spontaneous succession of loess vegetation in the region, e.g. by Molnár and Botta-Dukát, 1998). This phenomenon was typical not only for Central Europe, but also for other regions of the Palaearctic steppe zone (for example Kazakhstan or Russia; Dara et al., 2018; Prishchepov et al., 2021).

In total, 8 pristine and 5 recovered grassland fragments were selected for a detailed study, ranging from 0.5 to 1.0 ha in area. In 10 of them management ceased decades ago, whereas 3 are still extensively used by occasional mowing (Table 1). Sampled grasslands were located mostly in the lower part of the loess slopes, but there were grasslands on flat areas as well. Grasslands with different orientation were sampled to capture the highest variability in environmental conditions (Table 1). Pristine and recovered grasslands were classified using historical maps. Grasslands were classified as 'pristine' if grassland cover occurred continuously on consecutive maps since the time of the Second Military Survey (1863/64) (Timár et al., 2006, http://mapire.eu/hu/map/secondsurvey). Recovered grasslands spontaneously regenerated after former agricultural land use as crop fields, vineyards or orchards. We selected recovered grasslands that were typically 50 to 70 years old. The exact dates of abandonment could not be determined, but these grasslands were much younger than the identified pristine grasslands, and agricultural use ceased only after the Second World War. Maps were obtained from the Archives of Tolna county and included hand-drawn maps from the end of the 18th to the end of the 19th century.

2.2. Sampling setup

In each grassland site we designated five study areas of 10 m × 10 m in which plots of different sizes were embedded. We started the sampling at one corner and increased the plot size stepwise, following the nested-plot methodology proposed by Dengler et al. (2016) and Dengler et al. (2018), but using the following deviating plot sizes: 1) 10 cm × 10 cm, 2) 30 cm × 30 cm, 3) 50 cm × 50 cm, 4) 1 m × 1 m, 5) 2 m × 2 m, 6) 3 m × 3 m, 7) 4 m × 4 m, 8) 5 m × 5 m and 9) 10 m × 10 m. In each plot we recorded the coverage of each vascular plant species on a percentage scale. Nomenclature follows Király (2009).

2.3. Data capture and analyses

We extracted trait data of species from the Pannonian Database of Plant Traits (PADAPT; Sonkoly et al., 2023). We obtained data for life form, plant height, thousand-seed weight, seed bank type, clonality, rosette formation likeliness, leaf dry weight (LDW), leaf area (LA), specific leaf area (SLA) and leaf dry matter content (LDMC) (details given in Table 2). For clonal spread ability we used the CLO-PLA database and classified the species into four ordinal categories based on potential distance and speed of lateral spread (Klimešová et al., 2017; Table 2). We used both classical and functional diversity metrics to compare the vegetation diversity of pristine and recovered grasslands. We calculated species richness (S), Shannon diversity (H; Shannon, 1948), Pielou evenness (E; Pielou, 1975) and Berger-Parker dominance index (d; Berger and Parker, 1970). Pielou evenness is calculated as $E = H/\ln S$, where H is the Shannon diversity and S the species richness. The Berger-Parker dominance index, which is a simple measure of the relative abundance of the most abundant species, was calculated as $d = A_{max}/A_{total}$, where A_{max} is the abundance of the most abundant species and A_{total} the summarised abundance of all species present.

We also compared the variation of diversity indices across spatial scales (scale dependency) in pristine and recovered grasslands by studying species area relationships (SAR) using the power function (Arrhenius, 1921; Chiarucci et al., 2006) because the latter performed well in former comparisons including small plot sizes suggested by several authors (e.g. Turtureanu et al., 2014; Zhang et al., 2021) and its parameters are easy to understand. The power-law function reads $\ln S = \ln c + z \times \ln A$, where S is species richness and A the sampled area, and 'c' and 'z' are fitted parameters representing the number of species per sampled area (c) and the increment of the number of species with the increase of sampling area (z, 'steepness' of the curve), respectively. The c and z scores were compared between pristine and recovered grasslands using a GLMM (grassland type included as fixed factor, site identity as random factor). The fitting was done in R using the 'sars' package (R

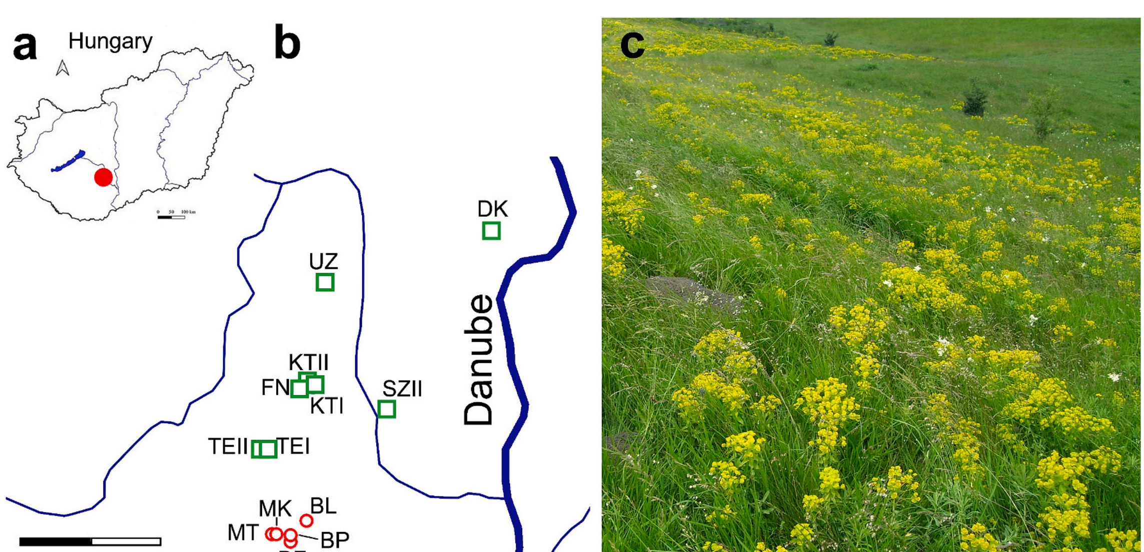

Fig. 1. Location of sampling sites (a, b) and photo of a pristine grassland site (c). Green squares denote the pristine and red circles the recovered grasslands. For the site codes and some further details of the sites see Table 1.

Table 1
Detailed information on sampling sites. For their geographical location see Fig. 1. Notations: Type: P – pristine grassland, R – recovered grassland; NA = no former agricultural cultivation to our knowledge, therefore pristine grasslands. Orientation: E = East, N = North, S = South, W = West, N/A = No slope inclination and orientation.

Site code	Nearest settlement	Type	Altitude (m)	Orientation	Slope (°)	Sampling date	Area (ha)	Management intensity	Cessation of the cultivation of arable crops
FN	Felsőnána	P	135	N	20	21.09.2019	0.5	No management in the last 15 years	NA
UZ	Uzd	P	140	N/A	0	10.09.2019	1.0	Low, occasional mowing	NA
MT	Majos (Temető)	R	135	W	30	26.09.2019	0.5	Low, occasional mowing	>50 years
MK	Majos (Katonai temető)	R	140	N/A	0	26.09.2019	0.5	Low, occasional mowing	>50 years
TEI	Tevel I	P	165	E	35	02.10.2019	0.5	No management in the last 15 years	NA
TEII	Tevel II	P	160	E	25	03.10.2019	0.5	No management in the last 15 years	NA
KTI	Kistormás I	P	110	W	10	14.10.2019	1.0	No management in the last 15 years	NA
KTII	Kistormás II	P	115	W	20	14.10.2019	0.5	No management in the last 15 years	NA
BF	Bonyhád Fáy telep	R	145	N/A	0	16.10.2019	0.5	No management in the last 15 years	>50 years
BP	Bonyhád, Prikk-lejtő	R	135	N	25	16.10.2019	0.5	No management in the last 15 years	>50 years
BL	Bonyhádlőtér	R	120	W	30	18.10.2019	1.0	No management in the last 15 years	>50 years
SZII	Szedres II	P	95	S	10	19.10.2019	1.0	No management in the last 15 years	NA
DK	Dunakömlőd	P	122	S	30	20.10.2019	1.0	No management in the last 15 years	NA

Table 2
Species traits used in the analyses.

Trait	Variable type	Values	Measurement unit
Clonal spread	Ordinal	1 = no clonal spreading, 2 ≤ 0.01 m/a, 3 = 0.01–0.25 m/a, 4 ≥ 0.25 m/a.	NA
Leaf area (LA)	Scale	Score	mm^2
Leaf dry matter content (LDMC)	Scale	Score	mg/g
Leaf dry weight (LDW)	Scale	Score	mg
Life form	Ordinal	1 = annual, 2 = biennial, 3 = perennial, 4 = semi-shrub/chamaephyte, 5 = phanerophyte	NA
Plant height	Scale	Score	cm
Rosette formation likeliness	Binary	1 = no rosette, 2 = rosette (or semi-rosette),	NA
Seed bank type	Binary	1 = persistent seed bank, 0 = transient seed bank	NA
Specific leaf area (SLA)	Scale	score	mm^2/mg
Thousand-seed weight	Scale	score	g

Core Team, 2010; Triantis et al., 2011; Matthews et al., 2022).

We also calculated the three components of functional diversity based on the traits listed in Table 2 (functional richness, functional evenness and functional divergence; Mason et al., 2005; Laliberté and Legendre, 2010). In addition, we calculated functional dispersion (FDis) to measure the functional similarity among the characteristic species of the species assemblages: high dispersion scores indicate high levels of niche differentiation and decreased levels of competition (Mason et al., 2005; Villéger et al., 2008). We calculated the community-weighted means (CWMs) of all single traits. All functional diversity calculations were done cover-weighted by using Gower distance measure and the FDiversity programme package (Casanoves et al., 2011). We analysed the effect of grassland type (binary variable) and plot size (repeated measure factor, 9 levels) in a two-way repeated measure LMEM (site identity was included as a random factor). We used SPSS 26.0 for the statistical analyses (IBM, 2019). We compared the vegetation composition of the sites using a DCA ordination in CANOCO 5.0 (ter Braak and Šmilauer, 2012). Ordination was based on the species abundance data of the largest (10 m × 10 m) plots. Indicator species analysis (IndVal) was applied to identify species typical for pristine and recovered grasslands (Dufrêne and Legendre, 1997). For the IndVal analysis we used the 'labdsv' package in an R environment (R Core Team, 2010; Roberts, 2010).

3. Results

We found that all but one species diversity metrics (species richness, Shannon diversity, Berger-parker dominance) were significantly affected by the grassland type: whereas the species richness and Shannon diversity were higher in pristine grasslands (Table 3; Figs. 2 and 3), the Berger-Parker dominance was lower (Fig. 4). For most of the multi-trait functional diversity indices, except for the functional divergence (higher in recovered grasslands, Fig. 7A), no significant effect of grassland type was found. Analysing the community-weighted means of single traits, we found that most traits were significantly affected by grassland type. Whereas the CWM of plant height (Fig. 5), life form (Fig. 7B), leaf dry weight (marginally significant, Fig. 7C), LDMC (Fig. 6) and thousand-seed weight (marginally significant, Fig. 7D) was higher in pristine grasslands, that of SLA (Fig. 7E), rosette formation likeliness (Fig. 7F) and seed bank type (Fig. 7G) was lower.

Species richness, Shannon diversity, evenness and Berger-Parker dominance were significantly scale-dependent in the studied grasslands (Table 3). Species richness and Shannon diversity were higher at all plot sizes in pristine grasslands (Figs. 2 and 3). Surprisingly, none of the multi-trait indices and most single-trait community-weighted means (except for plant height, LDMC and marginally thousand seed weight) showed a scale dependency effect (Table 3). We found that the 'c' parameter (number of species per sampled area) was significantly higher in pristine grasslands than in recovered ones ($p < 0.001$; estimated means are 3.163 and 2.393, respectively), whereas the 'z' parameter (the increment of the number of species with the increase of sampling

Table 3
Effect of grassland type (pristine or recovered), plot size and their interaction on species diversity, functional diversity and community-weighted mean (CWM) of single traits of the studied grasslands. Significant effects are denoted in **boldface** ($p < 0.05$), marginally significant effects ($p < 0.1$) in *italics* (Two-way repeated measure LMEM; repeated measure factor was the plot scale, while random factor the site identity).

Characteristic	Grassland origin		Plot size		Grassland origin × Plot scale	
	$F_{1,11}$	p	$F_{8,504}$	p	$F_{8,504}$	p
Species diversity						
Species richness	**51.144**	**< 0.001**	**705.762**	**< 0.001**	**111.011**	**< 0.001**
Shannon diversity	**63.427**	**< 0.001**	**53.374**	**< 0.001**	1.035	0.409
Berger-Parker dominance	**9.491**	**0.010**	**9.996**	**< 0.001**	1.247	0.269
Evenness	1.658	0.224	**8.667**	**< 0.001**	0.268	0.976
Functional diversity						
Rao entropy	1.427	0.258	1.197	0.299	**4.628**	**< 0.001**
Functional richness	0.626	0.445	1.061	0.389	1.016	0.423
Functional evenness	0.581	0.462	1.218	0.286	**4.703**	**< 0.001**
Functional divergence	**6.945**	**0.023**	0.609	0.771	0.545	0.822
Functional dispersion	0.673	0.429	0.590	0.786	1.491	0.158
CWM of single traits						
Life form	**7.596**	**0.019**	1.329	0.226	0.871	0.541
Plant height	**5.107**	**0.045**	**14.266**	**< 0.001**	**5.263**	**< 0.001**
Thousand-seed weight	*4.679*	*0.053*	*1.754*	*0.084*	**2.693**	**0.007**
Seed bank type	**5.467**	**0.039**	0.846	0.562	0.930	0.491
Clonality	1.388	0.264	1.151	0.328	**5.812**	**< 0.001**
Rosette formation	**5.903**	**0.033**	0.458	0.885	0.417	0.911
Leaf dry weight (LDW)	*3.909*	*0.074*	0.374	0.934	*1.920*	*0.055*
Leaf area (LA)	1.208	0.295	0.241	0.983	1.387	0.199
Specific leaf area (SLA)	**9.314**	**0.011**	1.676	0.102	0.514	0.846
Leaf dry matter content (LDMC)	**38.435**	**< 0.001**	**5.279**	**< 0.001**	0.391	0.925

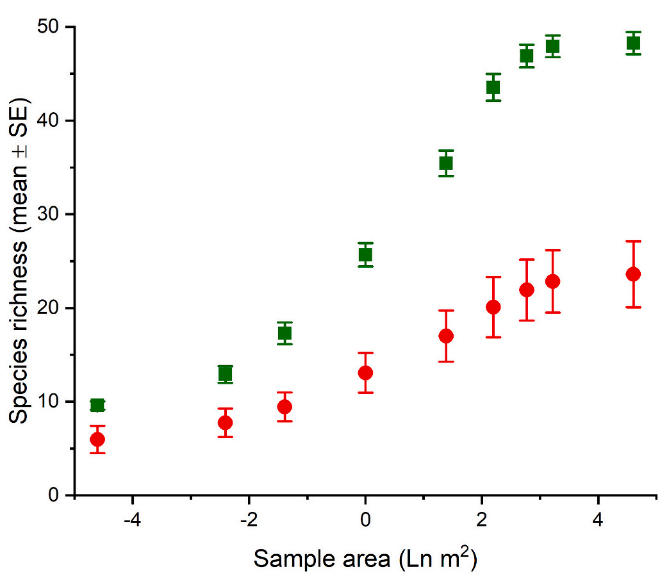

Fig. 2. Species richness in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means) across several plot sizes. Species richness is expressed as number of species. The plot sizes were 1) 10 × 10 cm, 2) 30 × 30 cm, 3) 50 × 50 cm, 4) 1 × 1 m, 5) 2 × 2 m, 6) 3 × 3 m, 7) 4 × 4 m, 8) 5 × 5 m, and 9) 10 × 10 m.

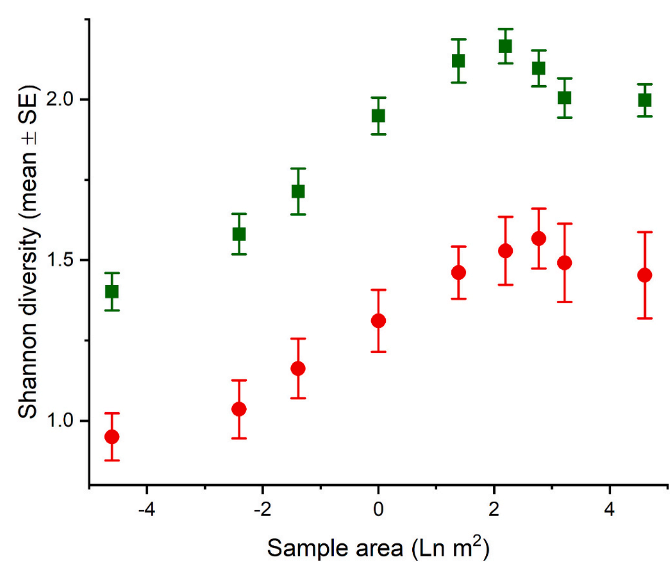

Fig. 3. Shannon diversity in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means) across several plot sizes. The plot sizes were 1) 10 × 10 cm, 2) 30 × 30 cm, 3) 50 × 50 cm, 4) 1 × 1 m, 5) 2 × 2 m, 6) 3 × 3 m, 7) 4 × 4 m, 8) 5 × 5 m, and 9) 10 × 10 m.

area, i.e. the 'steepness' of the curve) did not differ between the two grassland types ($p = 0.379$; estimated means are 0.208 and 0.195, respectively).

We found that there was a large difference in species composition between pristine and recovered grasslands as indicated by the clearly separated point clouds of pristine and recovered grasslands in the DCA ordination (Fig. 8). There was a similarly high variance detected in the species composition of the sampled stands of pristine and recovered grasslands. However, whereas the variation in the species composition for the recovered grassland stands was distributed along the first axis, the variation in case of pristine grasslands was along the second axis, and stands of this type of grassland formed two separated point clouds (Fig. 8). We found that there was an increase in species richness from primary to secondary grasslands distributed along the first axis in the DCA ordination. If we consider the orientation and slope inclination, we can see that the lowest diversity was associated with the two recovered grasslands on flat surface (BF and MK), whereas recovered grassland sites with a slope orientation and inclination were more species-rich, albeit not reaching the species richness of pristine grasslands. Such a clear separation in species richness based on orientation and slope inclination was not detected in case of pristine grasslands; however, two groups of sites were separated based on species composition along the second axis.

We identified 52 character species typical for pristine grasslands and

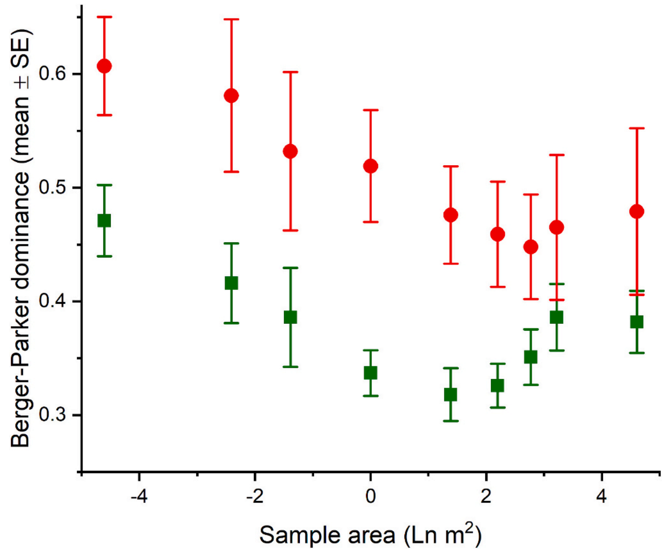

Fig. 4. Berger-Parker dominance in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means) across several plot sizes. The plot sizes were 1) 10 × 10 cm, 2) 30 × 30 cm, 3) 50 × 50 cm, 4) 1 × 1 m, 5) 2 × 2 m, 6) 3 × 3 m, 7) 4 × 4 m, 8) 5 × 5 m, and 9) 10 × 10 m.

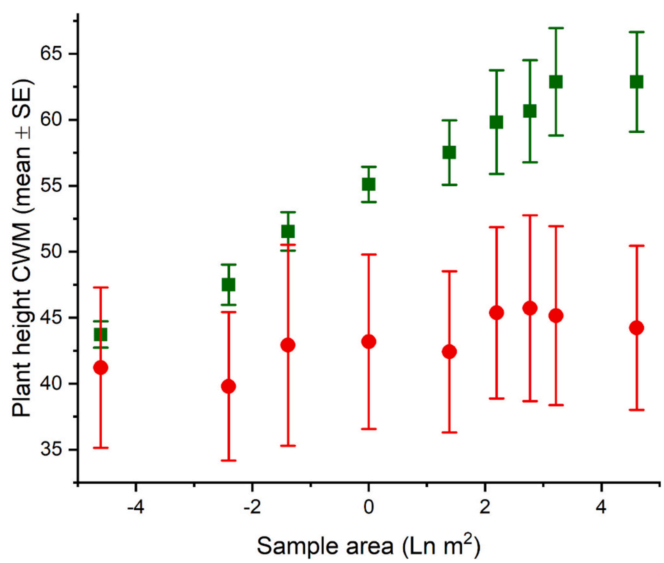

Fig. 5. Community-weighted mean of plant heights in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means) across several plot sizes. The plot sizes were 1) 10 × 10 cm, 2) 30 × 30 cm, 3) 50 × 50 cm, 4) 1 × 1 m, 5) 2 × 2 m, 6) 3 × 3 m, 7) 4 × 4 m, 8) 5 × 5 m, and 9) 10 × 10 m.

25 for the recovered ones (Appendices 1A and 1B). Several species of conservation interest were found among the character species of pristine grasslands (e.g. *Adonis vernalis*, *Inula germanica* and *Scabiosa canescens*), whereas disturbance-tolerant species (e.g. *Dactylis glomerata*, *Bellis perennis* and *Trifolium repens*) and several weeds (e.g. *Taraxacum officinale*, *Setaria viridis* and *Erodium cicutarium*) were characteristic for recovered grasslands (Appendices 1A, 1B and Fig. 8).

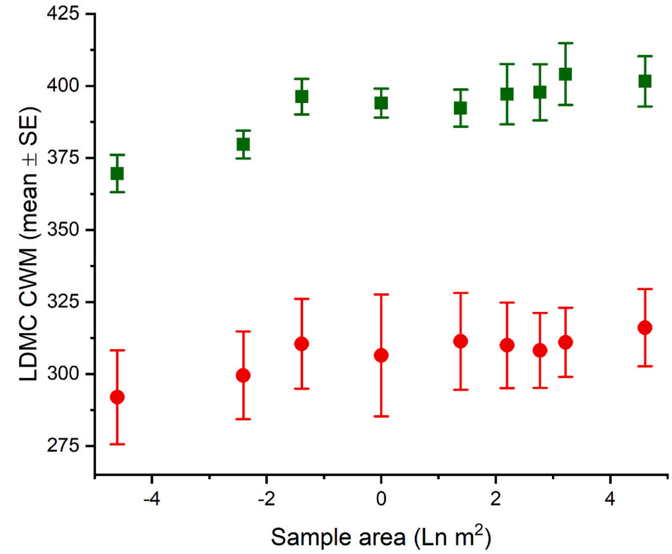

Fig. 6. Community-weighted mean of LDMC (Leaf dry matter content) in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means) across several plot sizes. The plot sizes were 1) 10 × 10 cm, 2) 30 × 30 cm, 3) 50 × 50 cm, 4) 1 × 1 m, 5) 2 × 2 m, 6) 3 × 3 m, 7) 4 × 4 m, 8) 5 × 5 m, and 9) 10 × 10 m.

4. Discussion

4.1. Unsuccessful full recovery of species diversity in recovered grasslands

We found that species richness and Shannon diversity were higher in pristine grasslands, emphasising that species diversity cannot recover within 50 years after the destruction of pristine grasslands. Similar results have been found by some other studies dealing with spontaneous secondary succession in loess and other types of steppic grasslands (e.g. Molnár and Botta-Dukát, 1998). One cause may be the very slow immigration rate of specialist species into old fields. Molnár and Botta-Dukát (1998) revealed that some grassland specialists, like *Potentilla arenaria*, *Filipendula vulgaris*, *Fragaria viridis* and *Thalictrum minus*, could not be detected in several-decades-old fields, despite their high abundance in the surrounding landscape (Molnár and Botta-Dukát, 1998). In spontaneously recovering alfalfa fields, generalist species colonised quite rapidly (within 10 years) after abandonment, whereas several grassland specialists including characteristic forbs remained absent, and the species richness remained to be lower than in reference pristine grasslands (Török et al., 2011b). Ruprecht (2006), however, found contrasting results and provided information on very successful establishment of dry grassland species in Romanian old fields. In that study it was found that in landscapes with a high proportion of species-rich grasslands and thus abundant propagule sources, only a very small fraction of target species was missing from the vegetation of the recovered grasslands after a couple of decades.

Another cause of the unsuccessful recovery of species diversity may be the increasing dominance of competitive generalist species, especially grasses, in the mid-phase (i.e. a few decades after the initiation) of recovered succession, which 'closes' the colonisation window and slows down or even blocks further recovery (Bartha et al., 2003; Albert et al., 2014; Bartha et al., 2014). This is in accordance with our finding regarding the Berger-Parker dominance, which was higher in recovered than in pristine grasslands, suggesting a high competitive pressure by one very abundant species in recovered grasslands.

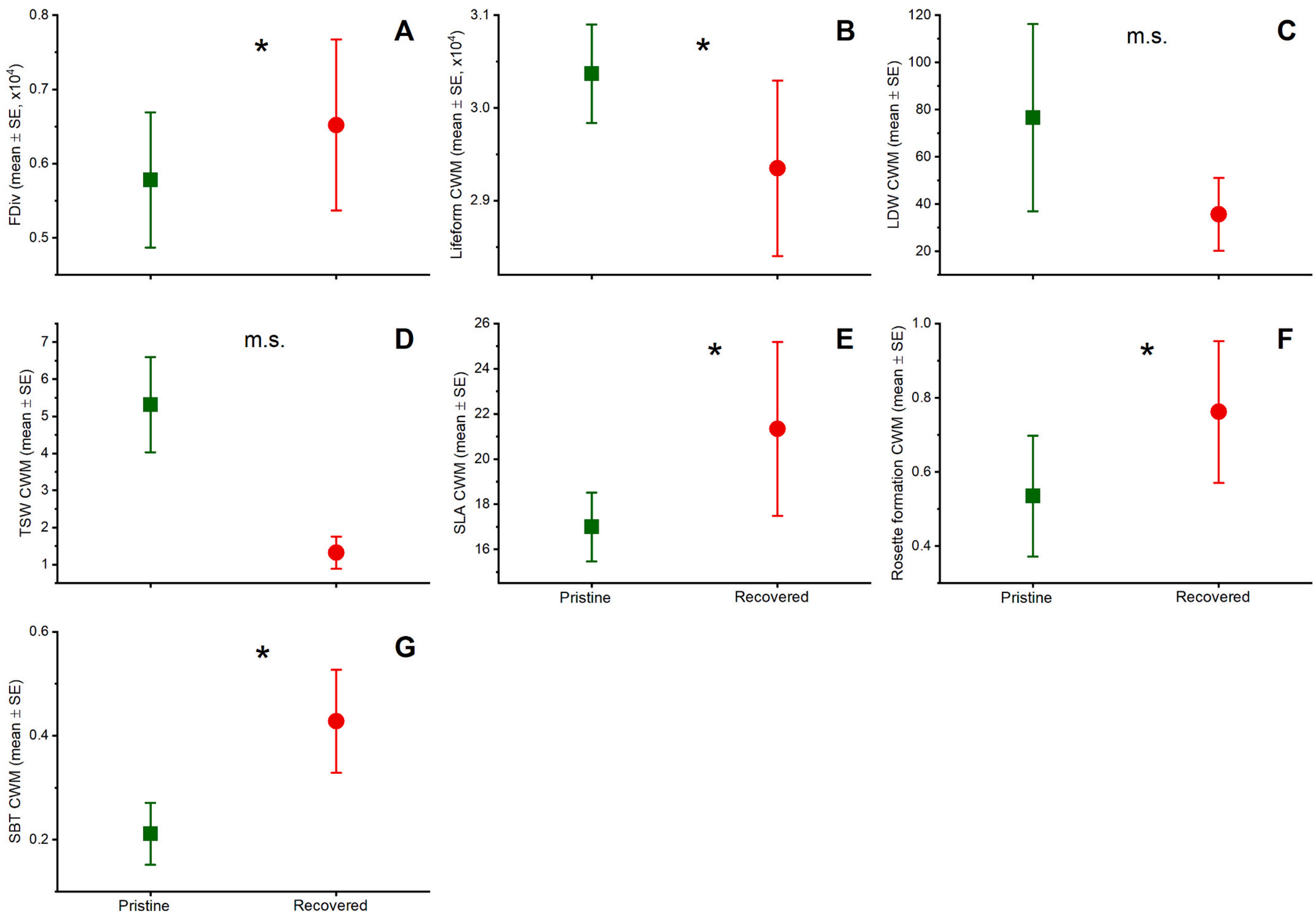

Fig. 7. Community-weighted means of various traits and functional characteristics in pristine (green rectangle) and recovered (red circle) grasslands (scatter plot with standard error bars, symbols show the means, calculated for the 10 × 10 m plots). Shown are only traits that were proven to be significantly (* - $p < 0.05$) or marginally significantly (m.s. - $p < 0.1$) different in pristine and recovered grasslands in the two-way repeated measure LMEM without showing scale dependency (for the detailed statistics see Table 3).

4.2. *Recovered grasslands are functionally as diverse as pristine grasslands*

Our results only partly confirmed the first hypothesis as grassland type had no significant effect on the multi-trait functional richness and evenness. Based on similar multi-trait functional richness and evenness of the recovered and pristine grassland stands, we infer that dry grasslands in our study area could recuperate relatively quickly (within 50 years) to well-functioning systems. Studying sand grassland and loess steppe restorations, Tölgyesi et al. (2019) found similar patterns: whereas functional diversity of spontaneously recovered sites became very similar to that of reference pristine grasslands, species richness was significantly higher in the latter. They proposed that functional diversity may recover much faster than species diversity, and this could explain the absence of significant differences in functional richness and evenness between pristine and restored grasslands. Rapidly colonising species may occupy important functions (niches) in reassembled grassland communities; however, functional redundancy remains to be waited for even after several decades. The low species richness even after 50 years of succession might be caused by the slow and rather stochastic immigration of species, which caused a higher functional divergence and likely lower functional redundancy in the recovered grasslands. In the face of future climate change or disturbances, functional diversity and functional redundancy of grassland plant communities are of outstanding importance. The disappearance of certain species will be less harmful to the functioning of the system if other species with similar traits take over their role.

In contrast to the results of Tölgyesi et al. (2019) we found the functional divergence to be higher and its variance to be much higher in recovered grasslands compared to pristine grasslands. It was also found that the recovery success of a characteristic species assembly is highly site-dependent (Ruprecht, 2006) and the formation of a mid-succession grass dominance highly species- and site-specific (Bartha et al., 2014). High functional divergence means that the most abundant species are located at the extreme ends of the functional range and the niche differentiation is high (Mason et al., 2005). A likely explanation for high functional divergence and its high variance in recovered grasslands is the lower stability of recovered grasslands compared to pristine grasslands. Former studies found that disturbance-driven immigration and disappearance of species are more common in recovered grasslands than in pristine grasslands (Bartha et al., 2003; Virágh and Bartha, 2003).

4.3. *Scale dependency of diversity patterns*

We found that in contrast to multi-trait functional diversity metrics, species richness and Shannon diversity were highly scale-dependent. However, across all the studied plot sizes the pristine grasslands were more diverse than the recovered grasslands. This finding was strengthened by the larger 'c' parameter of the SAR power function in pristine grasslands. These results do not support our second hypothesis about the scale dependency of differences in taxonomic and functional diversity measures between the two grassland types. The 'z' parameter of the SAR

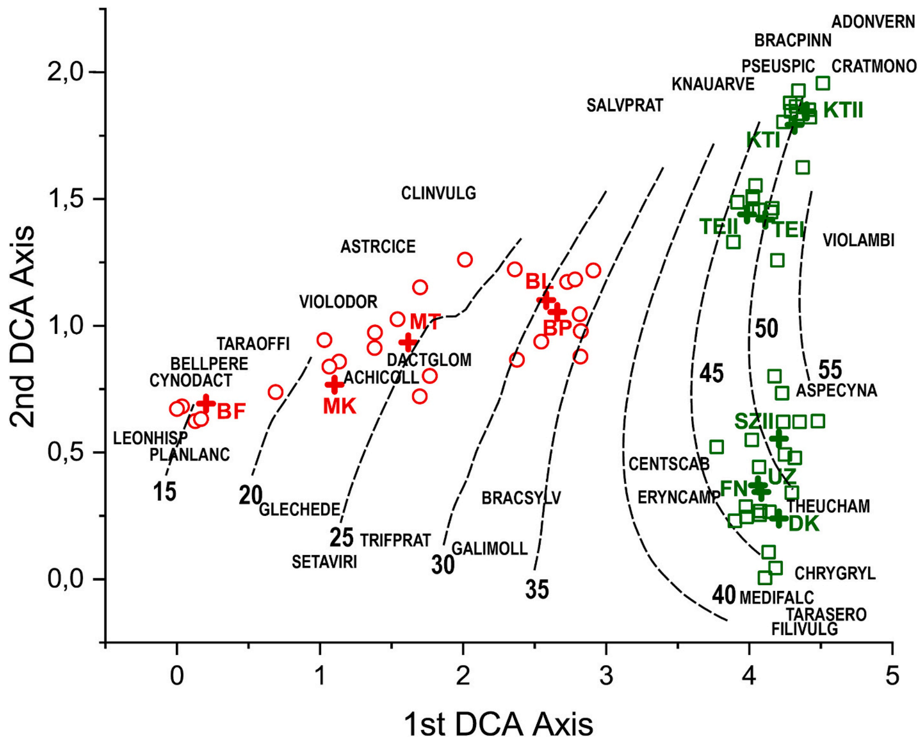

Fig. 8. Difference in the species composition of pristine and recovered grasslands displayed by a DCA ordination based on the species abundance data of the largest (10 m × 10 m) plots. Eigenvalues of the DCA are 0.696 and 0.245 for the first and second axes, respectively. Gradient lengths are 4.51 and 1.96 for the first and second axes, respectively. Cumulative species variance explained by the first four axes is 32.63. Dashed lines represent isolines for species richness (from 15 to 55). Green colours represent pristine, red colours recovered grasslands, with '+' denoting the centroids of the sites. Site codes are: FN: Felsőnána, UZ: Uzd, MT: Majos (Temető), MK: Majos (Katonai temető), TEI: Tevel I, TEII: Tevel II, KTI: Kistormás I, KTII: Kistormás II, BF: Bonyhád Fáytelep, BP: Bonyhád, Prikk-lejtő, BL: Bonyhád lőtér, SZII: Szedres II, DK: Dunakömlőd. 15 most characteristic species both for pristine and recovered grasslands identified by the IndVal analysis (highest IndVal scores) are shown. Species names are abbreviated to the first four letters of the genus and the first four letters of the specific epithet. For the complete list of species and abbreviations see Appendices 1A and 1B.

power function was not different between the studied grassland types, showing that the increase in species number with increasing plot size is not steeper in pristine grasslands than in recovered ones. Our 'z' values (0.195–0.208) fit well into the range reported in a loess grassland study with similar plot sizes by Turtureanu et al. (2014) (0.159–0.264). Similar 'z' values were obtained in other studies of dry grasslands and mesic meadows (Dengler, 2005; Chiarucci et al., 2006; Dolnik and Breuer, 2008). A much higher 'z' value (0.32) was reported in a study on loess grassland patches on kurgans by Dembicz et al. (2020); however, the area range in that study (from 107 to 4449 m^2) was quite different from ours.

4.4. Compositional differences between pristine and recovered grasslands

We hypothesised that there is a high compositional difference between primary and recovered grasslands. This hypothesis was confirmed by our results. It was also found by Nerlekar and Veldman (2020) that the species assembly process in recovering the habitat-specific species pool of pristine grasslands is slow and high persistence of weedy species is typical in recovered grasslands. In the present study we found much higher numbers of characteristic species for pristine grasslands than for recovered ones, and most characteristic species of recovered grasslands were disturbance-tolerant species or weeds. This pattern was also found by former research analysing successional patterns in recovered steppic loess and sand grasslands (Török et al., 2011b; Bartha et al., 2014; Albert et al., 2014).

As Fig. 1 shows, the sampled stands of pristine grasslands were distributed over a much larger area than the stands of recovered ones. Despite this, we found a similarly high compositional heterogeneity in pristine and recovered grasslands (Fig. 8). Neither the heterogeneity nor the spatial distinction of two groups of grassland stands in case of pristine grasslands can be explained by spatial arrangement and/or proximity of grasslands. These results might be an indication of the lower levels of organisation and lower compositional stability in terms of small-scale species fluctuations in recovered grasslands compared to pristine ones, as identified by some other studies (Bartha et al., 2003; Virágh and Bartha, 2003). It has been stressed that the species composition and assembly of a particular site is originate from different levels and types of filters (e.g. species pools and filtering concept of Zobel et al., 1998) and that compositional stability is also influenced by the landscape context driving various levels of colonisation credit or extinction debts (Cousins, 2009; Török and Helm, 2017). It was also found that the composition and diversity of grasslands cannot be explained based on the current spatial arrangement and proximity of grasslands or diversity of landscape, but past landscape composition is more likely responsible for the current patterns (Cousins et al., 2007). We have not analysed the local abiotic parameters (e.g. soil texture, nutrient availability, soil compactness or water regime) of sampled grasslands in detail. The sampled grasslands were variable in terms of slope orientation and inclination, but regardless of the differences in these variables, pristine and recovered grasslands appeared as distinct point clouds on the ordination graph (Fig. 8), and they had a markedly different species composition. Thus, potential differences in environmental factors between sampled grassland sites may have only a small influence on the species composition, not masking the main effect of grassland history.

However, not only was the species composition highly distinct, but also were most of the community weighted means of single traits significantly different between pristine and recovered grasslands. We found that pristine grasslands are characterised by taller, larger-seeded perennial species with higher leaf dry weight and leaf dry matter content. By contrast, recovered grasslands are characterised by rosette-forming species with a high SLA and a persistent seed bank. In line with these findings, Veldman et al. (2015) highlighted that many pristine grassland species are characterised by a long lifespan, low success at establishing from seeds, transient seed banks and persistent underground bud banks.

Dynamically stable communities favour long lifespan, intensive vegetative growth and reproduction and other characteristics providing a competitive advantage over others, like large plant height and large leaf area (Janečková et al., 2017; Deák et al., 2021b). These findings were also supported by the present study. Higher leaf dry matter content and lower specific leaf area are adaptations that enhance drought tolerance in harsh environments (Deák et al., 2021b; Lindborg et al., 2014). We found that LDMC was higher, whereas SLA was lower in pristine grasslands. Rosette-forming leaves are close to the soil surface and can capture light effectively when the community biomass is low. The ability to form rosettes is beneficial in highly disturbed habitats, where biomass production is rather low or the vegetation is intensively removed by mowing or trampled by intensive livestock grazing (Tóth et al., 2018).

Among the important drivers of compositional differences between pristine and recovered grasslands are seed weight and seed bank strategy. We found that in pristine grasslands the community-weighted mean of seed bank type was much lower (lower level of persistence), whereas that of seed mass was significantly higher than in recovering ones. Weeds and disturbance-tolerant species often form persistent seed banks, whereas characteristic perennial and stress-tolerant species of pristine grasslands generally have transient seed banks. This was validated for many grassland types in Europe including dry grasslands and mesophilous meadows (Bossuyt and Honnay, 2008; Kiss et al., 2016). Under more stable conditions, when gap formation by disturbance is less frequent, the production of large, but rather transient seeds are favoured over small, easily dispersed and persistent ones (Bossuyt and Honnay, 2008; Lindborg et al., 2014). Larger seeds grant competitive advantage during germination as higher reserves in large seeds enable a faster seedling development and larger seedlings, which provides advantage in early establishment and seedling competition (Leishman et al., 2000). The higher reserves of larger seeds enable seeds to germinate from deeper soil layers and seedlings to break through thicker litter layers and also improve the drought tolerance of seedlings (Janečková et al., 2017; Sonkoly et al., 2020).

5. Conclusions

Our results indicate that there are remarkable differences in taxonomic and functional diversity between pristine and recovered grasslands. These differences are clearly evident even after 50 years of grassland succession, indicating that the recovery of species-rich loess grasslands requires a long time. Our results also point out that during recovered succession there is a likely functional saturation of the species assembly in the first few decades of recovery, and while patterns and structure of recovered grasslands became quite similar to those of pristine grasslands, species richness and diversity still remained much lower. Pristine grasslands support considerable plant diversity, and species composition is slow to recover if destroyed by agricultural land use. This underlines the priority of protecting existing pristine grassland remnants over the recovery of destroyed ones. Restoration actions should focus first on enlarging the area of pristine grassland fragments and on buffering them with recovered grasslands to mitigate the negative influence of the surrounding croplands and other human-made habitats by embedding them into a less hostile matrix. It is also important to properly manage the pristine grassland fragments to preserve their high species richness; to fulfil this goal it would be important to sustain/introduce traditional management regimes in form of extensive grazing or mowing in these grasslands. Another important finding of our study is that unlike some taxonomic diversity metrics like Shannon diversity and species richness, most functional characteristics including single trait CWMs did not show scale dependency. This means that functional diversity metrics provide a good basis for the comparison of grasslands sampled with different plot sizes.

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CRediT authorship contribution statement

Péter Török: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Balázs Teleki:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **László Erdős:** Writing – review & editing, Methodology. **Andrea McIntosh-Buday:** Writing – review & editing, Methodology. **Eszter Ruprecht:** Writing – review & editing, Writing – original draft, Methodology. **Béla Tóthmérész:** Writing – review & editing, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

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.

Data availability

Data will be made available on request.

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Appendix A

Appendix 1A
Indicator species of the pristine grasslands identified by an indicator species analysis (IndVal) using abundance data of the largest (10 m × 10 m) plots. Species codes are composed of the first four letters of the genus and the first four letters of the specific epithet.

Species	Species code	IndVal score	Significance
Chrysopogon gryllus	CHRYGRYL	1.000	0.001
Teucrium chamaedrys	TEUCCHAM	0.975	0.001
Centaurea scabiosa	CENTSCAB	0.916	0.001
Brachypodium pinnatum	BRACPINN	0.880	0.001
Filipendula vulgaris	FILIVULG	0.880	0.001
Medicago falcata	MEDIFALC	0.868	0.001
Eryngium campestre	ERYNCAMP	0.853	0.001
Adonis vernalis	ADONVERN	0.851	0.001
Viola ambigua	VIOLAMBI	0.837	0.001
Salvia pratensis	SALVPRAT	0.825	0.001
Crataegus monogyna	CRATMONO	0.822	0.001
Asperula cynanchica	ASPECYNA	0.814	0.001
Knautia arvensis	KNAUARVE	0.759	0.002
Pseudolysimachion spicatum	PSEUSPIC	0.758	0.002
Taraxacum serotinum	TARASERO	0.742	0.001
Nonea pulla	NONEPULL	0.725	0.001
Botriochloa ischaemum	BOTRISCH	0.710	0.013
Hypericum perforatum	HYPEPERF	0.707	0.005
Galium glaucum	GALIGLAU	0.707	0.001
Euphorbia glareosa	EUPHGLAR	0.689	0.001
Tanacetum corymbosum	TANACORY	0.689	0.004
Sanguisorba minor	SANGMINO	0.685	0.002
Seseli anuum	SESEANNU	0.662	0.001
Cirsium boujartii	CIRSBOUJ	0.652	0.002
Trifolium montanum	TRIFMONT	0.652	0.001
Campanula bononiensis	CAMPBONO	0.632	0.001
Thymus glabrescens	THYMGLAB	0.632	0.007
Inula germanica	INULGERM	0.612	0.001
Serratula tinctoria	SERRTINC	0.612	0.002
Anchusa officinalis	ANCHOFFI	0.592	0.005
Ononis spinosa	ONONSPIN	0.592	0.002
Chamaecytisus austriacus	CHAMAUST	0.570	0.004
Elymus hispidus	ELYMHISP	0.569	0.039
Lathyrus tuberosus	LATHTUBE	0.556	0.015
Stipa capillata	STIPCAPI	0.548	0.008
Astragalus onobrychis	ASTRONOB	0.548	0.007
Peucedanum alsaticum	PEUCALSA	0.548	0.006
Thalictrum minus	THALMINU	0.524	0.007
Rapistrum perenne	RAPIPERE	0.524	0.011
Briza media	BRIZMEDI	0.524	0.005
Potentilla erecta	POTEEREC	0.514	0.031
Scabiosa canescens	SCABCANE	0.500	0.025
Artemisia campestris	ARTECAMP	0.500	0.010
Betonica officinalis	BETOOFFI	0.500	0.026
Rosa canina	ROSACANI	0.500	0.010
Senecio jacobea	SENEJACO	0.500	0.008
Stachys recta	STACRECT	0.500	0.010
Verbena officinalis	VERBOFFI	0.474	0.022
Senecio erucifolius	SENEERUC	0.447	0.039
Linum austriacum	LINUAUST	0.447	0.016
Prunella laciniata	PRUNLACI	0.447	0.013
Allium sphaerocephalon	ALLISPHA	0.418	0.037

Appendix 1B
Indicator species of the recovered grasslands identified by an indicator species analysis (IndVal). Species codes are composed of the first four letters of the genus and the first four letters of the specific epithet.

Species	Species code	IndVal score	Significance
Achillea collina	ACHICOLL	0.963	0.001
Taraxacum officinale	TARAOFFI	0.883	0.001
Cynodon dactylon	CYNODACT	0.872	0.001
Trifolium pratense	TRIFPRAT	0.807	0.001
Dactylis glomerata	DACTGLOM	0.791	0.002
Plantago lanceolata	PLANLANC	0.771	0.012
Glechoma hederacea	GLECHEDE	0.721	0.001

(*continued on next page*)

Appendix 1B (*continued*)

Species	Species code	IndVal score	Significance
Leontodon hispidus	LEONHISP	0.660	0.031
Astragalus cicer	ASTRCICE	0.650	0.008
Clinopodium vulgare	CLINVULG	0.646	0.024
Viola odorata	VIOLODOR	0.632	0.001
Bellis perennis	BELLPERE	0.600	0.001
Galium mollugo	GALIMOLL	0.569	0.005
Setaria viridis	SETAVIRI	0.566	0.002
Brachypodium sylvaticum	BRACSYLV	0.565	0.001
Potentilla arenaria	POTEAREN	0.560	0.034
Erodium cicutarium	ERODCICU	0.529	0.001
Erigeron annuus	ERIGANNU	0.517	0.005
Cichorium intybus	CICHINTY	0.447	0.004
Oxalis corniculata	OXALCORN	0.447	0.009
Prunus spinosa	PRUNSPIN	0.447	0.007
Trifolium repens	TRIFREPE	0.447	0.009
Calamagrostis epigeios	CALAEPIG	0.447	0.007
Tragopogon orientalis	TRAGORIE	0.432	0.025
Potentilla reptans	POTEREPT	0.346	0.045

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