Received: 4 December 2018 | Revised: 5 December 2019 | Accepted: 6 December 2019

DOI: 10.1111/avsc.12474

RESEARCH ARTICLE

Applied Vegetation Science IAVS

High resistance of plant biodiversity to moderate native woody encroachment in loess steppe grassland fragments

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Funding information
NKFIH (K 116639, K119225, KH 129483, KH 130320). HAS 'Momentum' Program (for the establishment of the MTA-DE Lendület Functional and Restoration Ecology Research Group)

Co-ordinating Editor: Norbert Hölzel

Abstract

Questions: Woody encroachment affects many open habitats from semi-deserts to wetlands and grasslands. We aimed to study the effect of native woody encroachment on grassland plant biodiversity in loess steppe fragments by analysing the vegetation composition of grasslands subjected to increasing levels of encroachment. We studied both ancient and restored grasslands with the following research hypotheses: (a) increasing woody encroachment decreases total diversity and the species richness of dry-grassland species; and (b) the effect of woody cover on grassland biodiversity differs between ancient and restored grasslands.

Location: South-Eastern part of Transdanubia, Hungary, Central Europe.

Methods: Altogether 63 loess grassland fragments were selected for the study. The percentage cover of trees, shrubs and herbaceous vegetation were recorded in 400-m^2-sized plots (n = 110). The effects of woody encroachment and grassland age on diversity, total species richness of the herb layer, and richness of dry-grassland species were analysed.

Results: We found that woody encroachment affected the total richness of the herb layer and the species richness of dry-grassland species. For most of the listed variables, lowest values were found for the highest woody encroachment groups. Grassland age affected the species richness of the herb layer and that of dry-grassland species; lower values were detected in restored grasslands. In restored grasslands, Shannon diversity and species evenness were lower, while Berger–Parker dominance was higher than in ancient grasslands. Species composition and richness displayed a relatively high resistance to moderate woody encroachment; the highest decrease in diversity was detected at a high level of woody encroachment (>52% of woody cover).

Conclusions: We can conclude that low to moderate woody encroachment cannot be simplistically regarded as degradation. Results suggest that moderately encroached loess grasslands can be easily restored by the suppression of woody species, as their species pool still contains many dry-grassland species targeted for restoration.

KEYWORDS
abandonment, biodiversity conservation, dry grassland, Festuco-Brometea, fragmentation, grassland restoration, grassland species, loess steppe, species diversity, woody encroachment

1 | INTRODUCTION

Woody encroachment is a worldwide phenomenon and occurs on many types of grasslands and open herb-dominated habitats, from semi-deserts to wetlands (Naito & Cairns, 2011; D'Odorico, Okin, & Bestelmeyer, 2012). Many studies have shown that woody encroachment is facilitated by: (a) general climatic change; (b) elevated atmospheric CO_2 concentrations; (c) atmospheric nitrogen deposition; (d) altered regime of natural disturbances (such as change in fire regime); and (e) altered frequency and intensity of management practices (Archer, Schimel, & Holland, 1995; Köchy & Wilson, 2001; Briggs et al., 2005; Knapp et al., 2008).

The strong effects of woody encroachment on ecosystem structure and functioning have been well documented (Dullinger, Dirnböck, & Grabherr, 2003; Komac, Kefi, Nuche, Escós, & Alados, 2013). Woody encroachment often results in ecosystem degradation with related biodiversity decline, and has considerable effects on net primary production, the cycling of surface water and nutrients, and carbon balance (Lett & Knapp, 2005; Knapp et al., 2008; Kesting, Wrage, & Isselstein, 2009; Maestre et al., 2009 and literature cited therein). More studies have focused on woody encroachment in semi-arid to semi-humid open habitat types from North America, South Africa and Australia (Cabral, Miguel, Rescia, Schmitz, & Pineda, 2003; Maestre et al., 2009; D'Odorico et al., 2012), whereas the Palaearctic has received less attention with most recent studies focusing on shrub encroachment in the Mediterranean region (but see Kesting et al., 2009 and Kesting, Petersen, & Isselstein, 2015 or Komac et al., 2013).

One of the most remarkable dry grassland types is the steppe, covering approximately 8.9 million km^2 in the central and eastern parts of the Palaearctic (Török, Wesche, Ambarli, Kamp, & Dengler, 2016; Wesche et al., 2016). Steppes of the western Palaearctic covering highly productive chernozemic soils were mostly transformed to croplands, and the decline of their former area often exceeds 90% (Wesche et al., 2016). Especially in lowland areas, only small fragments of these types of grasslands have survived in the form of small isolated midfield islets, road verges or on burial mounds (Deák, Tóthmérész, et al., 2016). Beside habitat loss, the most important driver of grassland biodiversity decline is the change of management intensity of grasslands (Török et al., 2018). In most lowland regions in the western Palaearctic, management intensity is increasing in highly productive grasslands leading to overuse such as overgrazing (Török & Dengler, 2018). Conversely, as the management of fragmented and isolated grasslands ceases to be profitable, they are often abandoned. Woody encroachment may occur following either management intensification or land abandonment (Fischer & Wipf, 2002; Ratajczak, Nippert, & Collins, 2012). In Central Europe, the biodiversity of most secondary dry-grassland communities is threatened by various types of woody encroachment caused by the cessation of former management by grazing or mowing (Elias, Hölzel, & Tischew, 2018; WallisdeVries, Poschlod, & Willems, 2002). Several authors argued that the re-introduction of traditional management is not sufficient to recover the former biodiversity of grasslands and in some cases mechanical clearing and measures that facilitate the species immigration and/or dispersal are necessary (e.g., Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010; Török, Vida, Deák, Lengyel, & Tóthmérész, 2011). From a restoration perspective, it is very important to know how resistant the biodiversity of dry grasslands to shrub encroachment is, and to have case studies that support decisions in the process of prioritising conservation and restoration (Török & Helm, 2017).

Another aspect that should be considered in restoration projects is grassland age and management history. It was stressed by Bartha, Meiners, Pickett, and Cadenasso (2003) and Virágh and Bartha (2003) that while ancient grasslands are highly organised in terms of species assemblages and also display high levels of stability to species turnover at small scale, secondary grasslands are less resistant, and their species pool is highly vulnerable to disturbances and species immigration. Thus, it can be expected that there could be differences in the response of their species composition to woody encroachment. Both aspects are crucial given that nature conservation authorities often lack funding to implement management activities. Thus, understanding processes and trends of species composition dynamics during woody encroachment for biodiversity conservation and restoration is vital.

In our research, we aimed to analyse the effect of native woody encroachment on dry-grassland plant biodiversity by analysing the vegetation composition of grasslands subjected to increasing levels of shrub encroachment. We investigated both ancient and restored loess grasslands with the following research hypotheses: (a) the increase of woody encroachment decreases grassland diversity and the species richness of dry-grassland species; and (b) grassland age (ancient or restored) modifies the effects of shrub encroachment on grassland biodiversity in the studied grasslands.

2 | MATERIALS AND METHODS

The study region is in the southeastern part of Transdanubia, Hungary, located in an area of 50 km radius in the vicinity of the towns Siófok, Székesfehérvár, Dunaújváros, Paks, Szekszárd and Pécs (Figure 1). The climate is moderately continental with a mean annual temperature of 10–11°C and annual precipitation of 550–600 mm with a high chance of extended summer drought periods (Mezősi, 2017). The studied grasslands are classified as 6250

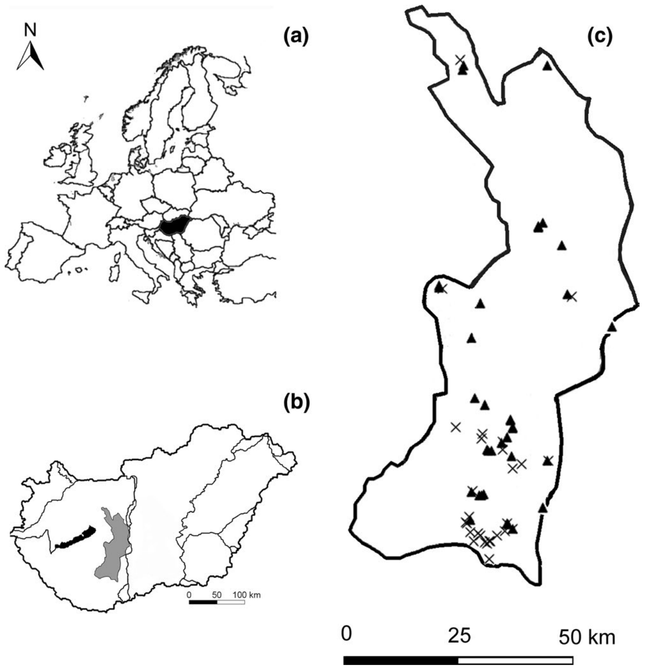

FIGURE 1 Sampling area. (a) Map of Europe with the location of Hungary (in black); (b) map of Hungary showing Lake Balaton (in black) and the study area (in grey); and (c) study area with the sampled ancient grasslands (triangles) and restored grasslands (crosses)

Pannonic loess steppic grasslands in the EU Natura 2000 system. They are characterised by several tussock-forming and stoloniferous grasses (e.g., *Agropyron cristatum*, *Bothriochloa ischaemum*, *Brachypodium pinnatum*, *Bromus erectus*, *B. inermis*, *Chrysopogon gryllus*, *Festuca pseudovina*, *F. rupicola*, and *Stipa* spp.), and a high number of forbs (e.g., *Euphorbia glareosa*, *Adonis vernalis*, *Salvia pratensis*, *S. nemorosa*, *Inula germanica*, *I. hirta*, *Thalictrum minus*, *Viola ambigua*, *Taraxacum serotinum*, *Thymus* spp.; Illyés & Bölöni, 2007). Ancient grasslands cover various types of loess deposits and are situated in naturally occurring forest steppe openings (Borhidi, Kevey, & Lendvai, 2012; Erdős, Ambarli, et al., 2018; Erdős, Kröel-Dulay, et al., 2018).

Within this study region we selected a total of 63 loess grassland fragments (35 ancient and 28 restored grasslands) ranging from 0.5 to 5 hectares (for the locations and other details see Appendix S1). Most of the selected grassland fragments have been abandoned for decades, while some were managed by low intensity or occasional cattle or sheep grazing before the study. In each grassland fragment, we sampled the vegetation in 400-m^2-sized plots ranging from 1 to 10 in number depending on the grassland area. We also took care to evenly cover grasslands with different exposition and slope in our study to avoid the confounding effect of these factors on the results. Altogether 110 plots were sampled and included in the analyses. In each plot, we recorded the cover of the tree and shrub layers and the vascular plant species composition of the herb layer using the Braun-Blanquet method and estimated the cover of species using a percentage cover scale (Dierschke, 1994).

Ancient and restored grasslands were classified using historical maps. Grasslands were classified as "ancient" if grassland cover occurred on consecutive maps continuously since the time of the Second Military Survey (1863–64). Grasslands that spontaneously recovered following former use as crop fields, vineyards or orchards (according to the military maps) were designated as "restored" grasslands. Maps were obtained from the Archives of Tolna County, including maps in manuscript from the end of the 18th to the end of the 19th centuries. Digitalised maps of the Second Military Survey were also used (Timár et al., 2006, http://mapire.eu/hu/map/secondsurvey). The studied loess grasslands in the region grow on chernozemic soils which are developed on loess bedrock. Loess grasslands were historically embedded in a mosaic landscape of the forest steppe zone (Erdős, Ambarli, et al., 2018; Erdős, Kröel-Dulay, et al., 2018). This historical landscape was characterised by dry loess grasslands, semi-dry grasslands both with and without shrubs, and fragments of open and closed steppic scrubs and forests. Because of the high suitability of chernozemic soils for agriculture, ancient loess vegetation has survived only on sites inappropriate for cultivation (e.g., steep valley sides, burial mounds), or on roadsides as verges (Deák, Tóthmérész, et al., 2016).

We sampled plots with increasing levels of woody encroachment (Table 1). Typical shrub species of various degrees of native woody encroachment were *Crataegus monogyna*, *Prunus spinosa*, *Cornus sanguinea*, *Ligustrum vulgare* and *Rosa canina*. In heavily encroached sites, several other native woody species were able to establish, such as *Ulmus minor*, *Quercus pubescens*, or *Fraxinus ornus*. In the studied grasslands only very low levels of invasive tree encroachment were detected, principally by the species *Robinia pseudoacacia* and *Celtis occidentalis*.

TABLE 1 Woody cover ranges included into woody encroachment ordinal groups 1 to 5 used in the analyses

Woody encroachment group	Number of plots	Mean cover of woody species (% ± *SE*)	Minimum cover of woody species (%)	Maximum cover of woody species (%)
1	22	13.50 ± 1.32	3.97	23.17
2	20	28.47 ± 0.68	23.18	32.28
3	18	42.50 ± 1.28	32.44	52.00
4	20	58.30 ± 0.85	52.19	64.00
5	20	76.67 ± 2.43	64.1	97.18

Note: Plots without any woody encroachment were also included in the analyses as woody encroachment group 0 (in total 10 plots, 5 plots sampled in ancient and 5 in restored grasslands).

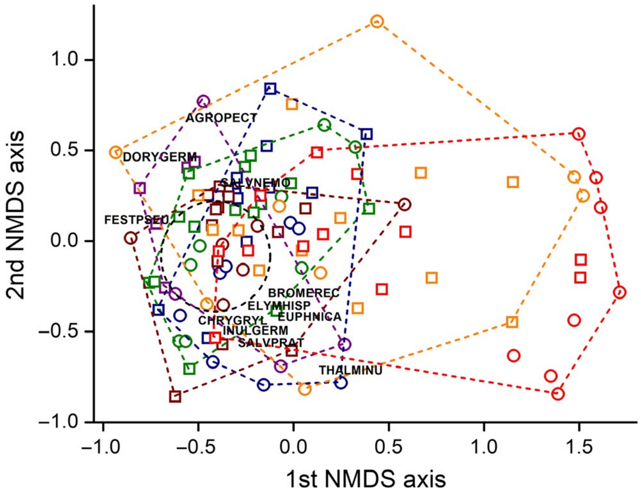

FIGURE 2 Vegetation composition of the studied grassland sites subjected to different levels of woody encroachment (NMDS ordination based on cover data of the herb layer and using Bray–Curtis similarity). Grassland age: rectangle = ancient grasslands, circle = restored grasslands. Levels of increasing woody encroachment: purple = group 0, control grasslands without any woody encroachment, green = group 1, blue = group 2, wine = group 3, orange = group 4, and red = group 5. For the woody cover ranges of each ordinal group see Table 1. Dry-grassland species in Appendix S2 are shown (25 dry-grassland species with the highest mean covers). We were not able to visualise all species; within the black circle, altogether 14 species are located as follows: FESTRUPI, BOTRISCH, BRACPINN, GALIVERU, AGRIEUPA, THEUCHAM, BROMINER, MEDIFALC, CHAMAUST, CENTSPIN, FRAGVIRI, CARECARY, THYMGLAB, and SCABOCHR

2.1 | Data processing and analyses

We classified the individual woody cover values to five woody encroachment groups on an ordinal scale, each containing 18–22 plots (woody encroachment groups 1 to 5, with 1 as the lowest and 5 as the highest level of encroachment, see Table 1 for cover ranges). In addition, we recorded as reference plots in grassland fragments without woody cover (five plots of ancient and five plots of restored grasslands, added as encroachment group 0). We estimated the cover of each woody species separately and for the establishment of woody encroachment groups we summarised these individual values. We merged the layers assuming an independent overlap according to Fischer (2015). For dry-grassland species, in line with the international literature, we considered the species of the class *Festuco-Brometea* (Dengler, Janišová, Török, & Wellstein, 2014). The group of "dry-grassland species" includes species considered diagnostic for the *Festuco-Brometea* class in the synthetic tables of the identification key of the Hungarian Flora by Simon (2000). Effects of woody encroachment and grassland age were analysed using two-way Generalized Linear Mixed Models (GLMM; Zuur, Ieno, Walker, Saveliev, & Smith, 2009); we assumed a normal distribution of dependent variables and used the identity link in SPSS 20.0 (IBM Corp., Armonk, NY, USA). In the analyses, "woody encroachment" (ordinal scale) and "grassland age" (nominal scale) were included as fixed factors with "site identity" as a random factor. We used the following as dependent variables: total richness of the vascular plant species in the herb layer (henceforth referred to as "total species richness"), richness of dry-grassland species, Shannon diversity, species evenness and Berger–Parker dominance (sensitive for the dominant species). Species evenness was calculated following Pielou (1975): $J_{\text{Evenness}} = H/\log(S)$, where H was Shannon diversity and S was the species richness. We calculated Berger–Parker dominance (d) based on the species abundances; the index was expressed by the proportion of the cover of the most abundant species from the total cover (d = [cover of most abundant species]/[total cover]) (May, 1975). Berger–Parker dominance is the highest (=1) in a community where there is a single species with 100% cover. It reflects well how "abundant" the species with the highest cover in the studied plot or community is. We used Fisher's Least Significant Difference (LSD) method for paired comparisons. To analyse the correlation of individual species abundances (expressed as cover values by each species in each plot) with the total species richness and woody encroachment, we

TABLE 2 Effect of woody encroachment and grassland age on the herb layer characteristics

	Woody encroachment		Grassland age		Interaction	
Characteristic	$F_{5,98}$	p	$F_{1,98}$	p	$F_{5,98}$	p
Species richness						
Total species richness	2.919	**.017**	7.303	**.008**	3.858	**.003**
Dry-grassland species	6.713	**<.001**	15.778	**<.001**	3.428	**.007**
Shannon diversity	0.492	.781	8.100	**.005**	0.677	.642
Species evenness	0.470	.798	4.088	**.048**	0.401	.847
Berger–Parker dominance	0.554	.735	5.726	**.019**	0.869	.505

Note: Significant effects (in bold) were detected using Generalized Linear Mixed Models, where "woody encroachment" (ordinal scale) and "grassland age" (nominal scale) were included as fixed factors, and "site identity" (= plots nested in sites) as random factor. Total species richness refers to the total richness of vascular plant species in the herb layer.

calculated Spearman rank correlation for the 25 most abundant herbaceous species (Appendix S2). To compare vegetation composition of the plots, we calculated NMDS ordination with Bray–Curtis similarity using the "vegan" package of R (R Core Team, R Foundation for Statistical Computing, Vienna, Austria). Plant nomenclature follows Király (2009).

3 | RESULTS

Altogether 346 species, including 113 dry-grassland species, were found in the herb layer of the studied grassland plots. In the ordination, we found that the species composition of the plots in the woody encroachment groups 0 to 3 were very similar, but in groups 4 and 5 the species composition became more heterogeneous (Figure 2). The abundance of 10 dry-grassland species out of the 25 dry-grassland species with the highest cover values were correlated positively with total species richness, while no negative correlations were detected (Appendix S2). In contrast, 12 species out of the same species group correlated negatively with woody encroachment and no positive correlations were detected (Appendix S2). This trend is also visualised by the NMDS ordination, where all of the 25 dry-grassland species were scaled to the point clouds of shrub encroachment groups 0 to 3 (Figure 2).

Total species richness and the species richness of dry-grassland species were significantly affected by woody encroachment (Table 2 and Figure 3). Total species richness showed an almost unimodal relationship with woody encroachment, with the lowest values detected in the woody encroachment group 5 (Figure 3a). The richness of dry-grassland species showed a continuous decrease along increasing woody encroachment, with a sharp decline at the encroachment groups 4 and 5 (Figure 3b). The total species richness and the richness of dry-grassland species were affected by grassland age; lower values for both were found in the restored grasslands (Figure 4).

None of the selected diversity and evenness measure shown in Figure 5 were affected by woody encroachment. In contrast, grassland age significantly affected Shannon diversity, species evenness and Berger–Parker dominance (Table 2). In restored grasslands, Shannon diversity and species evenness were lower, and the Berger–Parker dominance was higher than in ancient grasslands (Figure 6).

4 | DISCUSSION

4.1 | Woody encroachment and grassland age both drive species diversity

Woody encroachment negatively affected the species richness of dry-grassland species. Total species richness and the species richness of dry-grassland species were also affected by grassland age. Thus, our results supported both our hypotheses that: (a) the increase of woody encroachment decreases grassland diversity and the species richness of dry-grassland species; and (b) grassland age affects biodiversity patterns. The significant effects of the interaction between woody encroachment and grassland age on the species richness suggest that the species composition of ancient and restored grasslands may react differently to woody encroachment. The higher Berger–Parker dominance and lower species evenness typical of restored grasslands indicate that one or several community dominants (i.e., generalist graminoids and/or forbs) reach higher abundance in the restored grasslands than in ancient ones, which may affect the species composition and establishment processes at finer spatial scales suppressing subordinate species (Deák et al., 2015; Kesting et al., 2009).

We detected a significant effect of grassland age on the species richness and on the other studied diversity metrics using macro plots (400-m^2-sized) as suggested in the literature for comparisons of vegetation containing woody vegetation as well (Mueller-Dombois & Ellenberg, 1974). Other studies showed that differences between ancient and restored grasslands can be detected only at a much finer scale. For example, Dengler et al. (2014) stressed that at different spatial scales and grain sizes, different mechanisms are responsible for grassland biodiversity dynamics and that a large species pool at a greater scale does not necessarily equate to high species richness at the small scale and vice versa. This finding is supported by Dupré and Diekmann (2001), who studied grazed and abandoned dry basophilous grasslands and coastal meadows and found that beneficial effects of grazing on species diversity versus abandonment were detected at the small scale, but this effect diminished at larger grain sizes (100 to 1,000 m^2). Thus, we can expect that also in our study effects of higher levels of shrub encroachment on grassland species diversity are even worse at smaller spatial scale. There are some other assumptions that should be considered: (a) Woody encroachment may be more intensive in grasslands of secondary origin or degraded grasslands because the species pool of these types of grasslands is often smaller and therefore more susceptible to encroachment, Eldridge et al., 2011; Valencia-Gomez et al., 2015). (b) The age of restored grasslands should also be considered in the analyses, as it can also affect the resistance of woody encroachment. It was reported by several authors that large fluctuations in the species composition of secondary grasslands may occur, which can highly influence the present-day species composition and diversity of a restored grassland, especially if the grasslands are younger than 20 years (Bartha et al., 2014; Ruprecht, 2006). (c) It was also suggested by Dembicz et al. (2016) that area extent may also affect the diversity of grasslands. Our findings suggest that these could be valuable future research directions.

4.2 | Resistance of grassland biodiversity to woody encroachment

We found that the species richness and composition of the studied loess grasslands were highly resistant to moderate woody

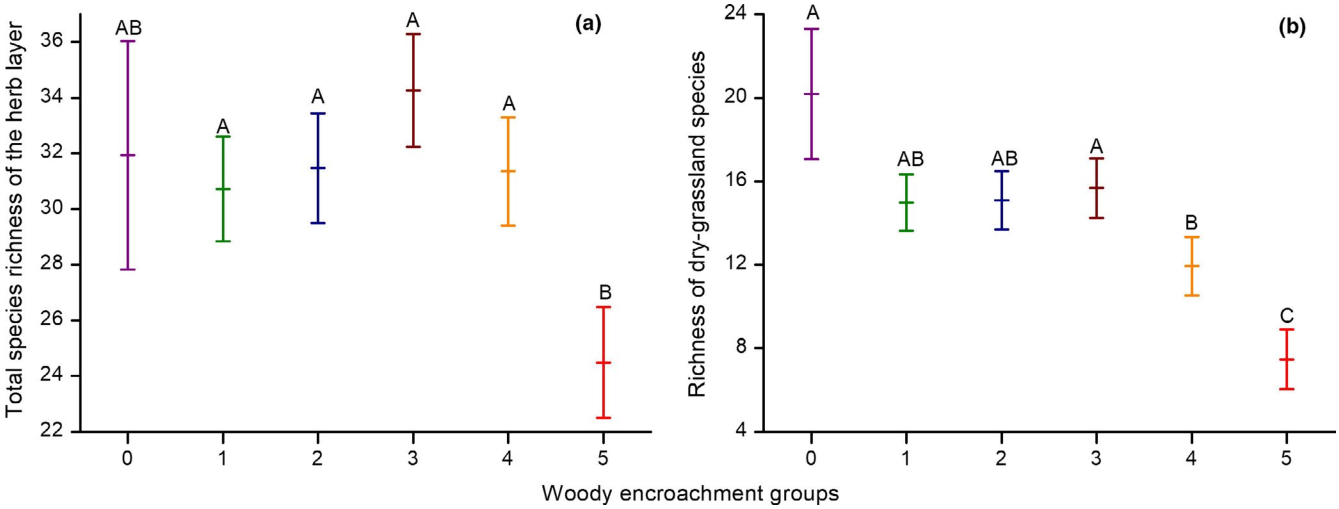

FIGURE 3 Estimated means (±*SE*) for species richness of respective groups of the herb layer in the different woody encroachment groups (significant differences are indicated with capital letters based on GLMM, LSD test for paired comparisons, <0.05). Panels: (a) Total species richness; (b) species richness of dry-grassland species. Colours follow the unified colouring used for the different woody encroachment groups throughout the whole paper, see explanations for Figure 2

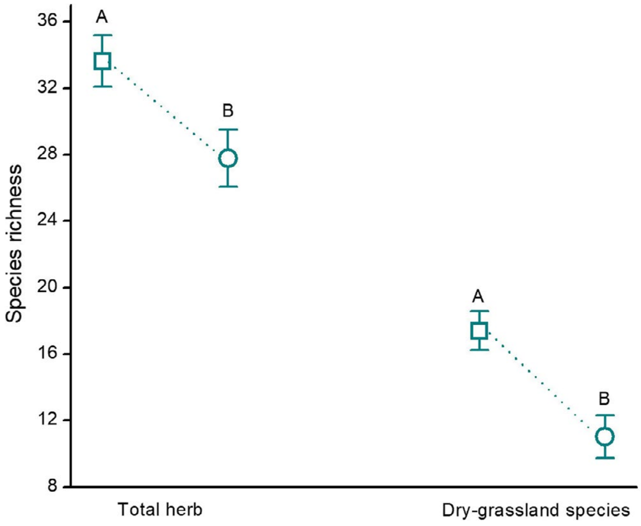

FIGURE 4 Estimated means (±*SE*) for species richness of the respective groups of the herb layer of ancient and restored grasslands. Grassland age: rectangle = ancient grasslands, circle = restored grasslands (significant differences are indicated with capital letters based on GLMM, and LSD test for paired comparisons, $p < .05$)

encroachment. A significant decrease in the richness of dry-grassland species and also marked changes in species composition were detected only in the two groups of highest woody encroachment in which the minimum of total cover of the tree and shrub layers was higher than 52%. Ratajczak et al. (2012) found that the response of species richness to woody encroachment in arid environments was of lower magnitude than in more humid environments. Moderate woody encroachment creates a more humid microclimate by providing shade, which produces suitable microsites for the establishment of many more mesic grassland species, especially in arid habitat types (D'Odorico, Caylor, Okin, & Scanlon, 2007; Gazol et al., 2012) but does at first not necessarily lead to a significant shift in species composition. Similar findings were made by Erdős, Bátori, Tolnay, Semenischenkov, and Magnes (2017) in forest/steppe mosaics of East-Austria, where the increase of woody cover caused by land-use changes did not immediately affect the species richness and cover of species characteristic to these habitat complexes.

The establishment of scattered trees and shrubs also increases the medium to large-scale habitat heterogeneity (see e.g., Zhou et al., 2019), which has proven to be beneficial for sustaining high species richness through providing multiple types of microsites for species establishment both for plants (Kesting et al., 2015, 2009; Tamme, Hiiesalu, Laanisto, Szava-Kovats, & Pärtel, 2010) and insects (Eldridge et al., 2011; Koch, Edwards, Blanckenhorn, Walter, & Hofer, 2015). In forest steppes, a heterogeneous habitat mosaic of grassland and forest patches in transition between closed forest and open grassland (Erdős, Ambarli, et al., 2018; Erdős, Kröel-Dulay, et al., 2018), most dry-grassland species can also grow near to shrubs and trees but some shade-tolerant and forest species are also favoured (Pykäla, 2005; Erdős, Tölgyesi, Körmöczi, & Bátori, 2015). With increasing cover of woody species, the area of fringe communities at the edge or transition zone between grassland and shrub- and/or tree-dominated vegetation increases, which could also be beneficial for biodiversity (Kesting et al., 2015; Erdős, Ambarli, et al., 2018; Erdős, Kröel-Dulay, et al., 2018).

It should be noted that we analysed only native woody encroachment while the encroachment of invasive woody species was low in our study grasslands. Contrary, Deák, Valkó, Török, and Tóthmérész (2016) reported for remnant grasslands on burial mounds woody encroachment, mostly by the invasive *Robinia pseudoacacia* as one of the most important local drivers of decline in species richness and cover of grassland specialist species.

Woody encroachment may occur due to changes in the management regime, for example the cessation of livestock grazing

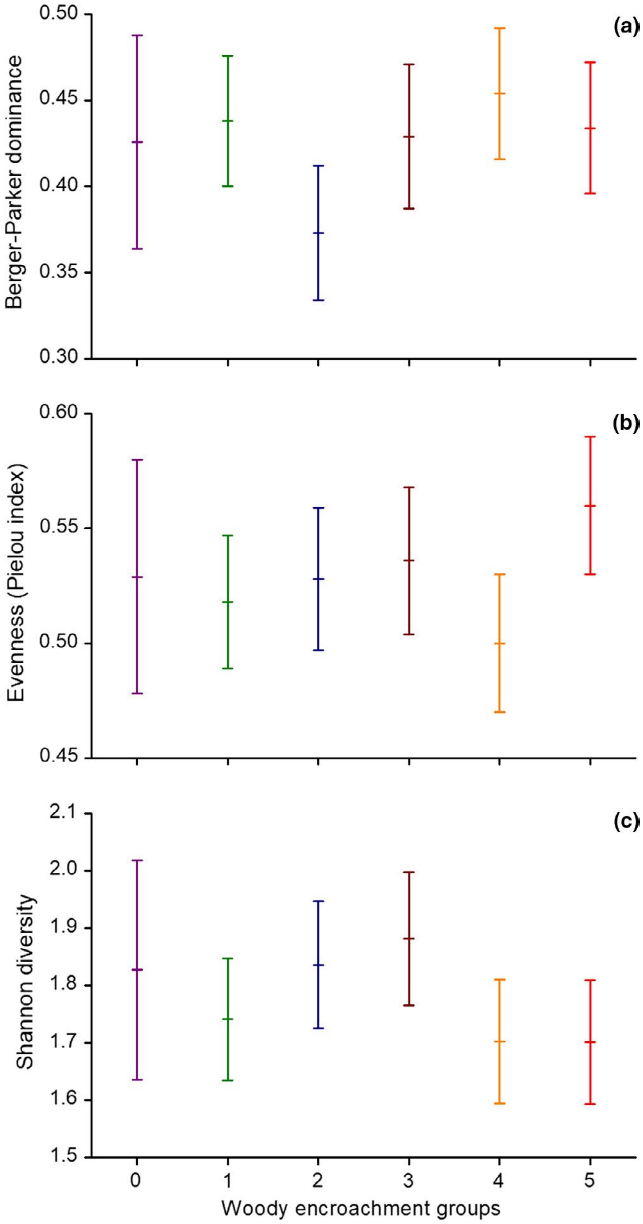

FIGURE 5 Estimated means (±*SE*) for diversity metrics in respective groups of the herb layer. Panels: (a) Berger–Parker dominance; (b) species evenness (Pielou index); and (c) Shannon diversity of the herb layer (no significant differences, analyses based on GLMM, and LSD test for paired comparisons, $p < 0.05$). Colours follow the unified colouring used for the different woody encroachment groups throughout the paper

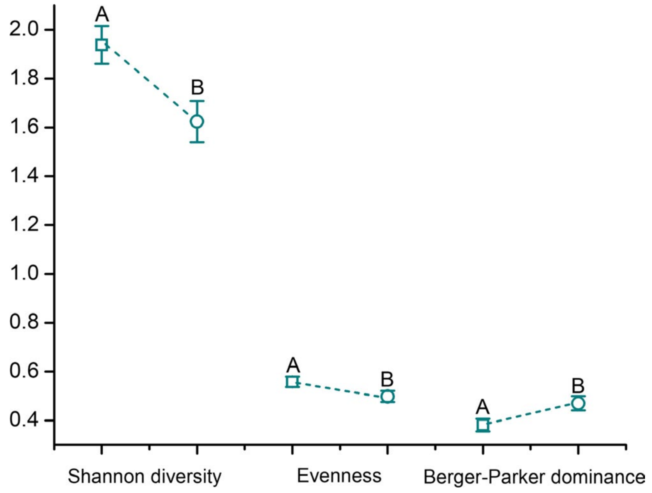

FIGURE 6 Estimated means (±*SE*) for Shannon diversity, evenness (Pielou index) and Berger–Parker dominance of the herb layer of ancient and restored grasslands (significant are indicated with capital letters based on GLMM, and LSD test for paired comparisons, $p < .05$). Grassland age: rectangle = ancient grasslands, circle = restored grasslands

(WallisdeVries et al., 2002; Elias et al., 2018). In several regions livestock grazing was reintroduced or intensified on various types of grasslands stimulated by agri-environmental subsidies (AES). In most cases, sheep grazing was introduced for various socio-economic reasons as it is generally much cheaper and easier to implement than cattle grazing (Baur et al., 2007; Varga et al., 2016). While reintroduction of grazing can be considered beneficial for grassland biodiversity in many grassland types, recent research indicated that high grazing intensity in loess grasslands can have detrimental effects on species richness and diversity. Török et al. (2018) found that following an increase in the intensity of grey cattle grazing from low (<1 livestock unit [LU] per ha) to intermediate grazing levels (up to 2.5 LU/ha), plant biodiversity of loess grasslands decreased by 50%. Another study (Tóth et al., 2018) indicated that sheep grazing should be avoided especially in grasslands with a high diversity and cover of forb species such as loess grasslands, as it can cause a strong decline in forb diversity even at low intensity levels. In contrast, in the case of low to moderate woody encroachment no such serious changes in composition and diversity were detected. Thus, in the case of loess grasslands moderate woody encroachment is a less severe threat to biodiversity than inappropriate grazing regimes that may be implemented to prevent woody encroachment.

5 | CONCLUSION

Woody encroachment is widely considered a serious threat to grassland biodiversity. In our study, negative effects of shrub invasion on grassland plant biodiversity were detected only at relatively high levels of encroachment. Other research has even found beneficial effects on local biodiversity through the creation of greater habitat heterogeneity (Kesting et al., 2015). Thus, low to moderate woody encroachment in dry loess grasslands by native shrubs and trees seems to be tolerable in the short term but requires control of mid-term successional processes, eventually followed by management interventions. Compared to plant diversity loss following land use intensification or improper conservation management even more strongly encroached sites hold a high restoration potential through shrub removal and adapted light livestock grazing as such sites usually still contain a sufficiently high proportion of the species pool of the target community.

ACKNOWLEDGEMENTS

The authors are indebted to Emmeline Natalie Topp for language revision of an earlier draft of the manuscript. The present study is a reference work for the LIFE-IP GRASSLAND-HU — Long term conservation of Pannonian grasslands and related habitats through the implementation of PAF strategic measures (LIFE17 IPE/HU/000018) project. The research was financed by the Higher Education Institutional Excellence Programme of the Ministry for Innovation and Technology in Hungary, within the framework of the 3. thematic programme of the University of Pécs. Authors are thankful to K. Virágh and S. Bartha for their advises and help. The authors are thankful to Norbert Hölzel for his editorial work and two anonymous reviewers for their suggestions to an earlier draft of the paper.

AUTHOR CONTRIBUTIONS

Balázs Teleki collected field data and initiated the research and manuscript writing, Péter Török and Béla Tóthmérész made the statistical analyses and Péter Török prepared the first draft of the manuscript. All authors revised the draft and improved the text.

DATA AVAILABILITY STATEMENT

The raw data for this publication are stored in the internal database of the MTA-DE Lendület Functional and Restoration Ecology Research Group. The authors will provide all data related to the paper upon request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

APPENDIX S1. Characteristics of the studied grasslands

APPENDIX S2 Correlation matrix of dry-grassland species (Festuco-Brometea species) with the woody encroachment and total species richness of the herb layer

How to cite this article: Teleki B, Sonkoly J, Erdős L, Tóthmérész B, Prommer M, Török P. High resistance of plant biodiversity to moderate native woody encroachment in loess steppe grassland fragments. *Appl Veg Sci*. 2019;00:1–10. https://doi.org/10.1111/avsc.12474