



## Nearby woody patches and microtopography reduce grass dieback during extreme drought

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### ABSTRACT

Extreme droughts related to climate change can be a driver of habitat transition by affecting the survival and reproduction of dominant plant species, while different microrefugia can buffer against this. The extreme drought of 2022 caused a significant dieback of the dominant perennial grasses in open sandy grasslands, in Hungary. We used this event to test our hypothesis: nearby woody cover and certain microtopography support the survival and recovery of dominant grasses after drought. We surveyed grass dieback in 200 plots within an unmanaged grassland site. A fine-resolution digital terrain model and aerial photos were used to determine topographic variables (slope, aspect, topographic position) and woody cover. We tested the effect of these factors on the ratio of dead grass and the amount of grass seedlings. Nearby woody cover had a significant sheltering effect: there was almost no grass dieback at high woody cover, modified by aspect and topographic position. High woody cover had the strongest effect on the northern aspect and on hilltops. While at low woody cover, aspect had no influence and valley position had a positive impact. The dead grass ratio was also lower on steeper slopes. Seedlings behaved differently: there were fewer seedlings on the more northern aspects and on steeper slopes, likely due to the lack of microhabitats available in the absence of grass dieback. We conclude that both woody cover and microtopography are important for survival and recovery of open sand grasslands, as they provide favourable microhabitats for grasses to survive extreme weather events.

### 1. Introduction

Climate change has a wide range of impacts on biodiversity and is expected to become more pronounced (IPCC, 2022). While the

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prominent feature of climate change is the global increase in average temperatures, it also induces changes in precipitation patterns (IPCC, 2021) that have an even larger potential effect on living organisms. Changes in precipitation patterns include the intensification of extreme events, such as storms or prolonged droughts. Extreme droughts, which are also becoming more frequent with climate change (Spinoni, 2018), have the potential to initialise ecosystem transformation. It has been recently shown that trends set the scene for ecosystem transition, while extreme events may initiate the transition itself (Orbán et al., 2023).

An extreme drought can lead to significant mortality of dominant plant species, a phenomenon previously underestimated due to the rarity of extreme droughts (Smith et al., 2024). If such an event occurs infrequently and is followed by weather conditions suitable for the recovery of the affected plant species, the system can reorganise itself (Lloret et al., 2012; Tielbörger et al., 2014; Orbán et al., 2023). However, with the increasing frequency of extreme events, the community may no longer withstand such impacts and could undergo a radical transformation, potentially causing a shift in ecosystems. Therefore, it is essential to understand the factors that contribute to the resistance or recovery potential of a particular plant community during extreme events (Orbán et al., 2023).

A notable means of recovery is recolonization from refugia, which can be understood at different scales. Originally, the term 'refugia' referred to places where species survived glaciations during the Last Glacial Maximum (Dahl, 1946), but recently the term has also been applied to safe havens from present and future climate change (e.g. Loarie et al., 2008; Keppel et al., 2012). Furthermore, the term 'microrefugia' has been used to refer to sites with locally different environmental conditions amidst surviving the - permanently or temporarily - unfavourable regional environments, and thus lower the dieback under extreme climatic conditions. As a consequence of this, species will be able to recolonize the surroundings of the microrefugia and maintain long-term viable populations on a larger scale (Rull, 2009, 2010; Godfree et al., 2011; Gentili et al., 2015). Such microrefugia may result from heterogeneous environments, such as small hills, local depressions or even woody patches (Fridley, 2009; Dobrowski, 2011; Gentili et al., 2015; Bátorfi et al., 2017).

In a mosaic landscape, as in the case of forest-steppe zones, microrefugia could have an important effect in mitigating climatic effects. Microrefugia can take biotic or abiotic forms. Grasslands as part of this zone are exposed to drought events and this exposure is expected to increase (IPCC, 2021). However, the proximity of forest patches has the potential to mitigate the drought effects by mitigating local microclimate (Süle et al., 2020; Erdős et al., 2021; Ho et al., 2024) and thus act as microrefugia. The presence of woody or shrubby vegetation can modify micro- or mesoclimate and thus provide more buffered environments for further types (De Frenne et al., 2013; Scheffers et al., 2014; Bátorfi et al., 2017). It has been shown that the forest patches in the forest-steppe zone, even the smallest, have an impact not only on the edge vegetation but also on the grassland components, thus potentially facilitating the grassland species to survive the extreme events (Süle et al., 2020; Ho et al., 2024).

Variation in microtopography presents microrefugia of abiotic origin and may affect the survival of grassland species as such (Alexander et al., 2016; Deák et al., 2017, 2021). As topography influences microclimate and soil formation, topographic variation allows both forest and steppe patches to occur beyond their macroclimatic niche, favouring the development of forest-steppe mosaics (Erdős et al., 2018; Chytrý et al., 2022). Topography-driven microclimatic spatial heterogeneity has been shown to have the potential to buffer the effect of climate change (Godfree et al., 2011; Bátorfi et al., 2017; Jiménez-Alfaro et al., 2024).

Thus both woody patches and microtopographic features have the potential to act as microrefugia, lowering the dieback during extreme events and providing safe sites for the germination and recovery of dominant plant species in a forest-steppe landscape. It is well-known that topography itself influences woody species establishment (Ukrainskiy et al., 2020; Aasberg, 2023); however, whether the presence of woody species modifies the effect of microtopography on species survival has remained unexplored. Similarly, the effect of microtopography – not on the establishment, but on the sheltering effectiveness – exerted by woody patches has not been elaborated yet.

The extreme drought event of 2022 at the KISKUN Long-Term Ecological Research (LTER) site at Fülöpháza, Hungary, where long-term monitoring of vegetation is conducted provides an opportunity to study both individual effects and interactions of microtopography and woody patches in an ecosystem highly exposed to drought stress (Kovács-Láng et al., 2000; Fekete et al., 2002; Mojzes et al., 2017; Orbán et al., 2023). Our goal was to explore the effects of this particular drought event on the vegetation. Specifically, we explored

- the magnitude of grass dieback and seedling emergence,
- the role of woody patches and microtopography and specifically their interaction in the reduction of dieback and in the germination of dominant species.

We hypothesised that microtopography and the cover of nearby woody vegetation jointly influence the variation in the response to drought.

## 2. Methods

### 2.1. Study site and field sampling

Vegetation data was collected in Central Hungary, in the Kiskunság National Park, near the village Fülöpháza (N 46.8774 – 46.8677; E 19.4016 – 19.4097) in a sandy grassland. These plots coincide with the monitoring plots of the Kiskun-LTER site (<https://kiskun.lter.hu/en>). Here 200 random plots were established in 2000 within a 50 ha area of open sand grassland and are regularly monitored (Rédei, 2005; <https://deims.org/dataset/19e6428c-4be8-41a8-9a54-a59a784b4a25>). Thus, a long-term record of its open sandy character and corresponding species composition exists. The dominant species of the grassland are tussock-forming grasses: *Festuca vaginata*, *Stipa borysthena* and *Koeleria glauca*. The study area is embedded in an approx. 150 ha semi-natural area,

which consists of a mosaic of open and closed grassland with small shrub and tree patches of *Populus alba*, *Juniperus communis* and *Crataegus monogyna* (Fig. 1).

The soil of the area is calcareous sandy soil with low humus content (below 1 %), high pH (8.09 in 0–10 cm) and high CaCO<sub>3</sub> content (11.1 % in 0–10 cm) (Kovács-Láng et al., 2000; Orbán et al., 2021). The climate is continental. Between 1961 and 1990 the mean temperature was 10.3 °C, and the mean annual precipitation was 504.5 mm, whereas between 2001 and 2023 these values were 11.3 °C and 584.5 mm, respectively (Kovács-Láng et al., 2000; Orbán et al., 2021, KISKUN LTER Fülöpháza Meteorological station, 2001–2023 (<https://kiskun.lter.hu/node/631>)). The differences in the two periods reflect a warming trend in the area with climate change.

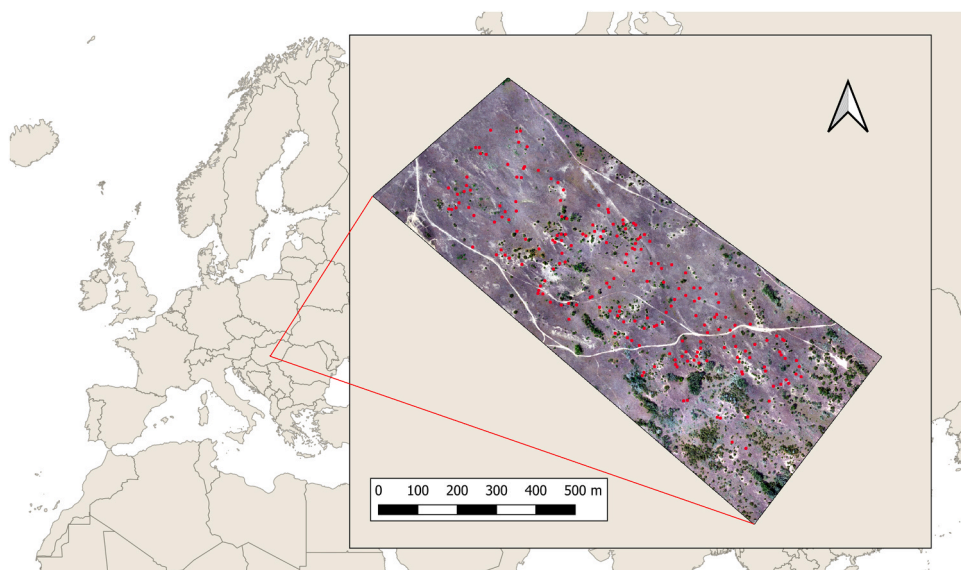
Even though the precipitation increased in recent decades, the increasing temperature and changing precipitation patterns resulted in several drought events. The severity of droughts can be characterised by the climatic water balance (P-PET) of a region. P-PET is calculated as the difference between precipitation (P) and potential evapotranspiration (PET). For a detailed description see Orbán et al. (2023) and Supplementary material 1). There were several drought periods between 1998 and 2023 (Fig. 2). In our case the P-PET showed significant depression in the year 2022 exceeding any droughts in the previous 20 years as identified by extending the analysis of Orbán et al. (2023).

In the 200 randomly placed, 4 m x 4 m LTER monitoring plots we surveyed (visually estimated) the aboveground cover of each vascular plant species (nomenclature: Király, 2009), separately the cover of young individuals of perennial grasses germinated in previous autumn (hereafter seedlings), the cover of cryptogam layer, the open soil surface, litter, and the dead grass tussocks in percentage in June of 2023.

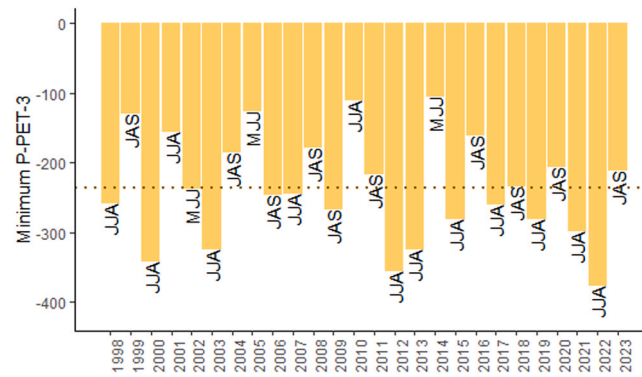
Microtopography was assessed by a remote sensing-based survey dedicated to this project using a UAS (Unmanned Aerial System) including a DJI Matrice M200 drone with a Zenmuse X5S RGB camera and a 15 mm F1.7 ASPH lens. The aerial survey was carried out on 24 June 2023, when the UAS image acquisition was performed from 120 m height above ground level. This yielded a 3 cm/pixel resolution RGB orthophotomosaic photo of the area and a digital surface model reconstructed by the SfM (Structure-from-Motion) method (Eltner and Sofia, 2020). Based on the classification algorithms applied on the SfM point clouds, we have generated the DTM (Digital Terrain Model, elevation of the ground surface) and the DSM (elevation of the ground surface + vegetation height) (Supplementary material 2). Vegetation plots were marked with plastic signs and their coordinates were also recorded using the orthomosaic. 5 of the 200 survey points were not possible to be identified from the orthomosaic, therefore, for these plots, GPS coordinates were recorded on the ground. Resolutions and projections of the remote sensing and field survey datasets were unified before further analysis. The Hungarian National Projection (HD72 / EO, EPSG 23700) was used in mappings throughout the study.

## 2.2. Data processing and analysis

We analysed the effect of microtopography parameters and cover of woody patches on the ratio of dead tussock-forming perennial grass (hereafter: dead grass) and the cover of seedlings of tussock-forming perennial grass (hereafter grass seedling). Dead grass ratio was expressed as the ratio of dead grass cover divided by the sum of living and dead grass cover. In this study, the grass cover (both living and dead) was estimated as the sum of the cover of three dominant, tussock-forming perennial grass species: *Festuca vaginata*, *Koeleria glauca* and *Stipa borysthénica*.



**Fig. 1.** Location of Hungary in Europe, the study area within Hungary as the origin of lines pointing to the orthophoto insert and the 200 vegetation plots in the study area.



**Fig. 2.** Minimum values of three-month climatic water balance (P-PET-3) in each year within the growing season (Apr-Sep) between 1998 and 2023 at the study site. P-PET characterises the severity of droughts of a region. P-PET is calculated as the difference between precipitation (P) and potential evapotranspiration (PET). For detailed description see [Orbán et al. \(2023\)](#) and [Supplementary material 1.](#)) Letters indicate the months when the minimum occurred (JJA: June-July-August, JAS: July-August-September, MJJ: May-June-July).

The cover of grass seedlings (namely the seedlings of *Festuca vaginata*, *Koeleria glauca* and *Stipa borysthenica*) was the second response variable of this study. The seedling cover values were recorded as percentages and were divided by 100 before the analysis to match the data range handled by the beta distribution.

As explanatory variables, we considered microtopographic variables on plot level and the cover of woody species in 10 m buffers around the plots.

Microtopographic variables were calculated for the entire drone imagery made for the studied 60 ha first. Aspect and slope were calculated within each vegetation plot, relying on the eight neighbours of each cell of raster image (hereafter: cells), then averaged for the plot. Since the resolution of orthomosaic photo was 10 cm, it was the mean of  $40 \times 40 = 1600$  cells for each plot.

The **aspect** values were transformed to represent an NNE-SSW gradient by applying the following function ([Kumar et al., 1997](#) as in [Somodi et al., 2010, Eq. 1](#)):

$$asp.val = (\cos(\text{aspect} - 22.5) + 1) / 2 \quad (1)$$

For **slope**, the mean of the cells within each vegetation plot was calculated. Topographic Position Index (hereafter **TPI**) was calculated first for the entire DTM raster with a rectangle-shaped 4 m x 4 m focal window, then the mean, the standard deviation and the minimum-maximum difference of the TPI were assessed within each vegetation plot ([Table 1](#)).

The cover of woody species was assessed according to the following steps. First, the difference between the DTM and DSM rasters was calculated. As there are no buildings in this area, this difference is an indicator of vegetation height. Based on visual inspection and expert opinion, 0.5 m was identified as a threshold above which cover can be attributed to woody species in the locality. The digital elevation model-based vegetation height indicator was inspected against the matching RGB orthomosaic to check whether any trees or shrubs were missing in the digital elevation model-based assessment: in this case, missing patches were manually added in QGIS. Percentage cover of woody vegetation was assessed in circles with a 10 m radius around the centre of each vegetation plot. Based on our previous field experience, woody vegetation has an effect on the plot in this distance through e.g. shading, diffuse radiation and soil fertilisation.

All explanatory variables were centred and tested for pairwise correlation by the Pearson correlation coefficient. High ( $>0.7$ ) correlations were identified between **TPI\_sd** and **TPI\_dif** ([Table 2](#)). We decided to keep **TPI\_sd**, since the effect of variation in topography on plant survival is more straightforward than that of the range of topographic positions. **TPI\_dif** was removed from the starting variable set.

Before constructing the final model, the multicollinearity structure was also inspected by the Variance Inflation Factor (VIF) from the car package ([Fox and Weisberg, 2019](#)). The VIF of the candidate explanatory variables – aspect, slope, woody, tpi\_mean, tpi\_sd – were checked and no further multicollinearity was found ( $VIF < 2$ ). Generalised linear models with the “ordbeta” link function were chosen for modelling according to the ratio nature of the response variables. We also considered all variables except for **TPI\_dif**, due to

**Table 1**

Abbreviations and short definitions of the explanatory variables used in the models.

Abbreviation	Definition
aspect	the mean aspect (of NNE-SSW gradient) within the vegetation plot
slope	the mean slope within a vegetation plot
woody	woody cover percentage in 10 m radius around the centre of vegetation plot
TPI_mean	the mean topographic position index within the vegetation plot
TPI_sd	the standard deviation of the topographic position index within the vegetation plot
TPI_dif	the difference of maximum and minimum topographic position index within the plot

**Table 2**

Correlation matrix of explanatory variables, showing the Pearson correlation coefficients. Bold letters indicate high correlation (0.7 and above), the limit above which correlation is considered to corrupt models and thus initiates variable pre-selection.

	aspect	slope	woody	TPI_mean	TPI_sd	TPI_diff
aspect	1					
slope	0.100	1				
woody	-0.074	0.153	1			
TPI_mean	-0.001	0.191	-0.127	1		
TPI_sd	0.005	0.499	0.096	0.347	1	
TPI_diff	0.028	0.556	0.111	0.307	<b>0.934</b>	1

correlation and their pairwise interactions (Table 2). As explanatory variables coincide for the two different models, these considerations are identical for both response variables.

Thus, the final model structure was:

response ~ aspect + slope + woody + TPI\_mean + TPI\_sd +  
 aspect:slope + aspect:woody + aspect:TPI\_mean + aspect:TPI\_sd +  
 slope:woody + slope:TPI\_mean + slope:TPI\_sd +  
 woody:TPI\_mean + woody:TPI\_sd +  
 TPI\_mean:TPI\_sd,

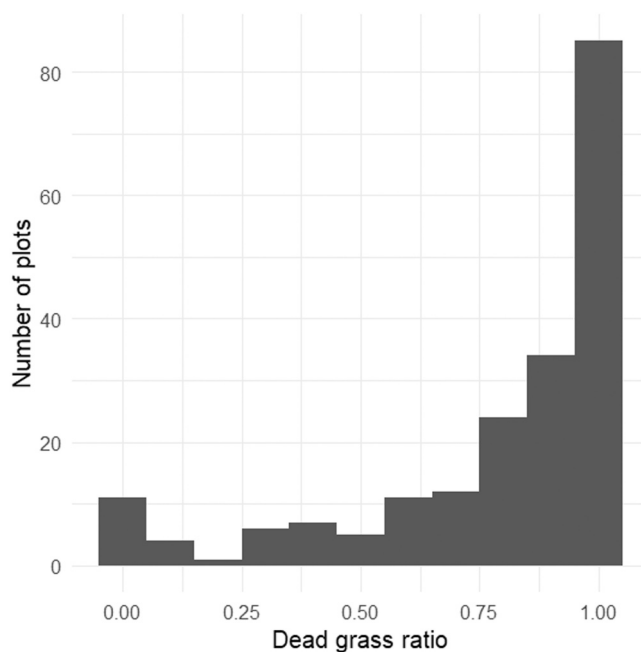
where response was dead grass ratio and grass seedling cover in the two separate models.

All data processing and analysis were performed in R language for statistical computing (R Core Team, 2022). We used the ‘raster’ package for operations involving rasters (Hijmans, 2022), the ‘spatialEco’ for TPI calculation (Evans and Murphy, 2023), the ‘glmmTMB’ package for model building (Brooks et al., 2017), the ‘DHARMa’ package for model diagnostics (Hartig, 2022) and the ‘performance’ package for multicollinearity (Lüdecke et al., 2021).

### 3. Results

#### 3.1. Dead grass ratio

In the majority of the plots ( $n = 167$ ), more than half of the grass cover was dead grass (dead grass ratio = 0.5). Average dead grass



**Fig. 3.** Histogram of dead grass ratio in the studied vegetation plots. Dead grass ratio was calculated as the ratio of dead grass cover divided by the sum of living and dead grass cover. Total number of plots was 200.

ratio was 0.78 in vegetation plots and reached higher than 0.95 in 85 plots out of 200 (Fig. 3).

The model outcome identified three variables with significant main effects on dead grass ratio at the study site and two significant interactions (Table 3).

From the main effects, only the 'slope' was not involved in interactions and thus its effect can be interpreted individually. Increasing slope steepness appeared to decrease the ratio of dead grass in plots (Fig. 4). The cover of woody vegetation in the 10 m buffer of the plots appeared to be influential, however, its effect was modified by the aspect and topographic position (Fig. 5). In general, the nearby woody cover decreased the dead grass ratio (i.e. dieback), however, the sheltering effect was enhanced by the north-northeastern aspect (expressed by higher values in our modified aspect variable), while the effect of woody cover could emerge only at high cover values in more southern aspects (Table 3, Fig. 5a, b).

The topographic position exerts a slight cross-over interaction. With almost no woody cover, there is less grass dieback in valley positions than in hilltops. However, already from ca. 15 % woody cover, woody cover has a larger sheltering effect on hilltops than in valleys (Fig. 5c, d).

### 3.2. Grass seedlings

The model built to explain the cover of emerging grass seedlings identified two significant main effects and no significant interaction (Table 4). More northern aspects appeared to reduce the cover of emerging grass seedlings. Steeper slopes also significantly reduced the cover of grass seedlings. In the meantime, the cover of woody vegetation in the 10 m buffer did not have any effect on the cover of grass seedlings.

## 4. Discussion

Extreme drought events are becoming more and more frequent (Spinoni et al., 2018; Kis et al., 2023) and have the potential to trigger ecosystem transitions (Rondeau et al., 2013; Orbán et al., 2023). Hungary is particularly exposed (Kis et al., 2023) and, thus unfortunately presents opportunities to study its effects. The extreme drought of 2022 at our study site provided an opportunity for deeper insight into the drivers of these changes. Woody cover and microtopography are known to influence the survival chances of vegetation in case of drought (Yao et al., 2006; Hawthorne and Miniati, 2018; Liu et al., 2020; Zang et al., 2020). In our study, woody vegetation and microtopographic variables together proved to be important in influencing the pattern of dieback of dominant perennial grasses that emerged after an extreme drought. Microtopography was relevant to both mitigate grass dieback and to influence seedling emergence after extreme drought, which is in concert with existing literature (Bennie et al., 2006; Liu et al., 2020; Yao et al., 2006; Zang et al., 2020), while woody cover influenced only grass dieback.

### 4.1. Factors affecting the dead grass ratio

There was less perennial grass dieback on steeper slopes, which could be explained by more humidity streaming down to and into the soil, especially when grass individuals died already on the flat hill tops. Moreover, steeper slopes with east-north and west aspects get less radiation than the same places with flat positions (Swift and Knoerr, 1973), which may also explain the higher proportion of grass surviving on steeper slopes.

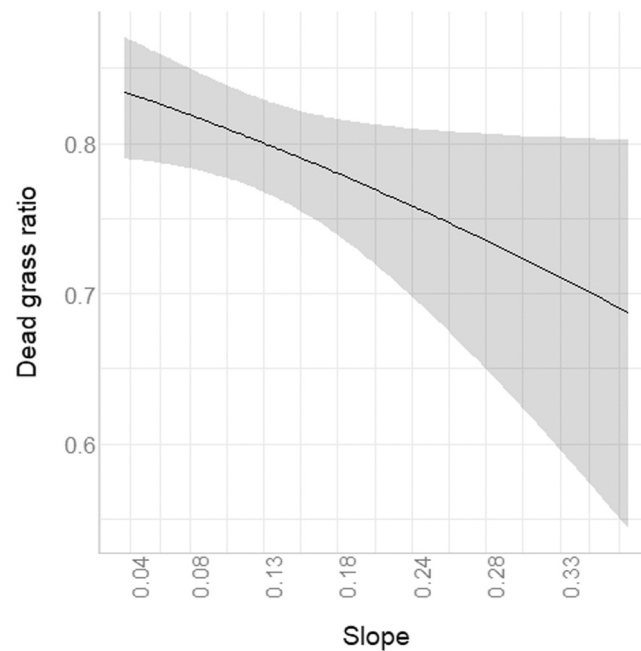
Grass dieback was markedly reduced in the presence of woody cover and in north-northeastern exposure, in a complex interaction relationship between woody cover and the aspect.

Woody cover and more north-northeastern aspects enhanced each other's influence. To such an extent, that aspect in itself, did not

**Table 3**

Summary table of the model for dead grass ratio. For variable names and definitions please consult Table 1. Bold indicates significant results. Statistical significances of variables are denoted: ns:  $p > 0.05$ , \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , and \*\*\*:  $p < 0.001$ .

	Estimate	Std. Error	z value	Pr (> z )	
(Intercept)	1.3887	0.0979	14.180	<2e-16	***
aspect	-0.7764	0.2631	-2.950	<b>0.0032</b>	**
slope	-2.4385	1.2056	-2.023	<b>0.0431</b>	*
woody	-13.4310	1.4108	-9.520	<2e-16	***
TPI_mean	4.7642	3.8182	1.248	0.2121	
TPI_sd	-3.3598	5.8149	-0.578	0.5634	
aspect:slope	-3.3114	4.0742	-0.813	0.4164	
aspect:woody	-10.1263	3.6193	-2.798	<b>0.0051</b>	**
aspect:TPI_mean	-7.2078	12.1140	-0.595	0.5518	
aspect:TPI_sd	24.3460	19.1202	1.273	0.2029	
slope:woody	-36.2266	21.6239	-1.675	0.0939	.
slope:TPI_mean	-13.8729	45.5759	-0.304	0.7608	
slope:TPI_sd	-72.0320	58.5792	-1.230	0.2188	
woody:TPI_mean	-104.0871	48.4229	-2.150	<b>0.0316</b>	*
woody:TPI_sd	145.9813	93.0425	1.569	0.1167	
TPI_mean:TPI_sd	-38.4414	207.0859	-0.186	0.8527	



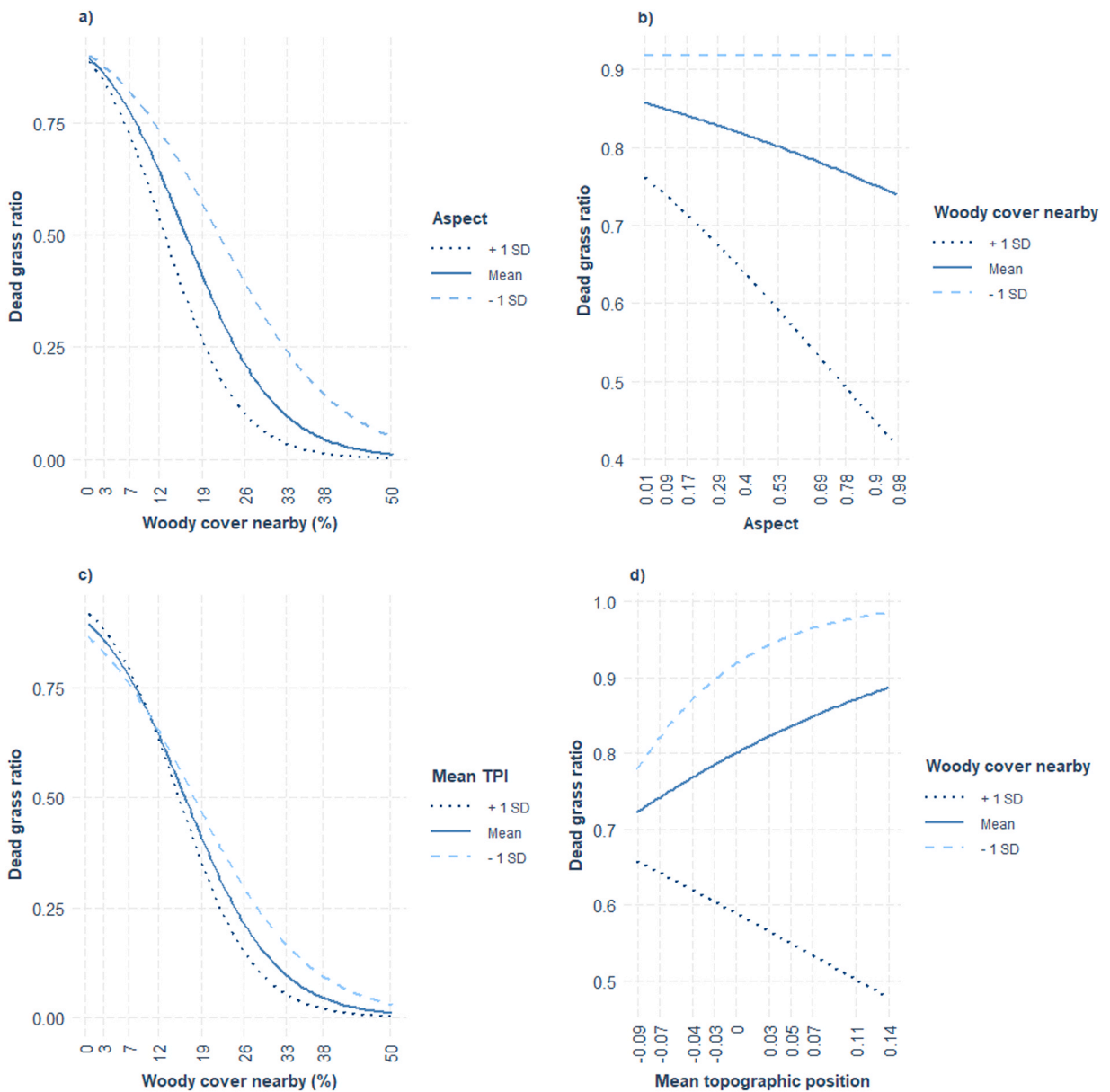
**Fig. 4.** Relationship between the slope and the dead grass ratio. Solid line expresses the partial response of dead grass ratio to changes in slope. Grey areas represent the 95 % confidence interval.

influence the level of grass dieback in the absence of woody cover. However, in the presence of even average woody cover, which is ca. 6 % in our case, a strong effect of aspect emerged. The more northern and northeastern aspect the plot had, the stronger the sheltering effect of nearby woody cover appeared to be. The most favourable position was the northeastern aspect with woody patches nearby, which highly corresponds to expectations (e.g. based on Yao et al., 2006; Zang et al., 2020) as water availability is highest in such positions together with lower air temperature and higher air humidity.

The effect of the dune aspect is well explicable by the general solar radiation pattern in the northern hemisphere, where western slopes receive direct solar radiation in the afternoon (Fu and Rich, 1999), when air temperatures are high. Consequently, eastern and northern slopes are usually cooler and wetter than the western and southern slopes (Hanks and Dick-Peddie, 1974; Holland and Steyn, 1975). Zang et al. (2020) also identified higher soil water content in the soil and a lower reduction in it after extreme drought on eastern slopes. Thus, in the event of extreme drought they exhibit microrefugia for the grasses as also underlined by our results. In the light of these earlier findings, it is slightly unexpected that the climate change mitigating effect of the northern aspect was only detectable if woody patches were also present nearby. The sandy substrate with low water holding capacity (Kessler and Oosterbaan, 1974) and the mild slopes in our study area probably mask the differences in soil water content. However, the presence of woody patches modifies the soil and increases water holding capacity (Chandregowda et al., 2018). In the presence of woody vegetation soils can potentially hold more water, which is a possible mechanism to explain how woody patches near northern aspects may disproportionately support grasses in the event of an extreme drought.

Nearby woody patches, besides influencing water availability (Duniway et al., 2010), may also influence the drought survival of grasses by modifying land surface temperature. It has widely been shown that both landscape composition and configuration have an effect on land surface temperature (Zhou et al., 2011; Du et al., 2016; Szulczewska et al., 2014). These studies also concluded that in coarse-textured vegetation, which typically included some level of woody vegetation, woody patches have significant cooling effect on their surroundings (Zhou et al., 2011; Du et al., 2016; Ho et al., 2024; Szulczewska et al., 2014). The sheltering effect of nearby woody patches could have included such a cooling effect as well, which is also plausible to be stronger in north-northeastern aspects. Besides the potential cooling effect, woody patches can exert an effect on the soil properties by the larger amount of litter. The litter layer, in turn, can have an effect on the soil water retention capacity.

Interestingly, the woody cover had also a cross-over interaction with the topographic position in our system. Valleys only had an extra value added to the presence of woody patches if the woody cover was low. Valleys offering shelter against drought is a pattern usually perceived due to excess water accumulating in these landforms (Crave and Gascuel-Odoux, 1997; Rodríguez-Iturbe and Porporato, 2007). Furthermore, depressions in the landscape, such as dolines or cool-air pods have been shown to act as climate change refugia for various species (Bátori et al., 2021; Nadeau et al., 2022; Pastore et al., 2022). However, in the presence of any noticeable woody cover (>12 %), the sheltering effect of the woody cover was more pronounced at the hilltop than in the valley, which seems to contradict expectations. We have to note that valleys in this landscape are very shallow (5–10 m) and thus valley effect may not be pronounced for this reason already. However, the valley effect can also be ecosystem-specific. Soil has likely more clay content at the bottom of the local valleys and higher sand content at the hilltop as Zang et al. (2020) also measured in a similar landscape. Sala et al. (1988) proposed the inverse soil texture hypothesis to explain seemingly counterintuitive biomass patterns like ours. According to



**Fig. 5.** Interactions in the model of dead grass ratio (y axis). a) Modification of the effect of the woody cover in a 10 m neighbourhood by the aspect of the location. Aspect is linearised according to Equation 1. +1 SD corresponds to more NNE, -1 SD to more SSW aspect. Effect of woody cover is enhanced in NNE aspects, while reduced in SSW aspect. b) Modification of the effect of the aspect by woody cover in a 10 m neighbourhood. +1 corresponds to NNE aspect, 0 to SSW. +1 SD corresponds to more woody cover, -1 SD to less woody cover. NNE aspect has no effect on dead grass ratio unless woody cover is present in the neighborhood. c) Modification of the effect of the woody cover in the 10 m neighbourhood by the mean topographic position (Mean TPI). Woody cover is in percentages. +1 SD corresponds to more hilltop position, -1 SD to more valley position. The interaction is of cross-over type, the interaction effect is small. d) Modification of the effect of mean topographic position by woody cover in a 10 m neighbourhood. Low TPI indicates valley position, high TPI hilltop position. +1 SD corresponds to more woody cover, -1 SD to less woody cover. Woody cover has opposite effect on dead grass ratio in valleys and hilltop position. Woody cover only reduces dead grass ratio (i.e. shelters against extreme drought) in hilltop positions.

their hypothesis, when precipitation is  $< 370$  mm/year (which is comparable to that at our site at drought events), sandy soils with low water-holding capacity are more productive than loamy soils with high water-holding capacity. The explanation is that loamy soils have relatively higher infiltration rates which reduce evaporative water losses. The inverse soil texture hypothesis also possibly explains our case, why the hilltop position with its more sandy soil can enhance sheltering effect by woody species. However, we also want to emphasise that TPI was not influential as a main effect, thus this impact is only exerted in interaction with the presence of woody species.

**Table 4**

Summary table of the model for grass seedling cover. For variable names and definitions please consult Table 1. Bold indicates significant results. Statistical significances of variables are denoted: ns:  $p > 0.05$ , \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , and \*\*\*:  $p < 0.001$ .

	Estimate	Std. Error	z value	Pr (> z )	
(Intercept)	-5.9865	0.0764	-78.34	<2e-16	***
aspect	-0.5958	0.1866	-3.19	<b>0.0014</b>	**
slope	-2.6138	0.9454	-2.76	<b>0.0057</b>	**
woody	-2.0339	1.0407	-1.95	0.0507	.
TPI_mean	1.1835	2.8227	0.42	0.6750	
TPI_sd	1.1539	4.6327	0.25	0.8033	
aspect:slope	4.7290	3.0494	1.55	0.1210	
aspect:woody	2.4271	2.6499	0.92	0.3597	
aspect:TPI_mean	-11.3999	9.3018	-1.23	0.2204	
aspect:TPI_sd	10.5945	14.8407	0.71	0.4753	
slope:woody	6.1291	17.6822	0.35	0.7289	
slope:TPI_mean	0.7164	38.4434	0.02	0.9851	
slope:TPI_sd	6.2135	45.6961	0.14	0.8918	
woody:TPI_mean	53.5469	41.5754	1.29	0.1978	
woody:TPI_sd	-63.0545	63.5966	-0.99	0.3215	
TPI_mean:TPI_sd	-109.6877	160.2694	-0.68	0.4937	

As the above sections also revealed, the effects of microtopography on vegetation patterns has widely been studied. There is also accumulated evidence that the margin of woody patches has a distinct microclimate (Jakucs, 1968; Davies-Colley et al., 2000; Erdős et al., 2014). Much less information is available on the effect of woody patches not directly at the spot, but in the broader landscape outside cities (Cadavid-Florez et al., 2019; Reis et al., 2022). These two examples both stress that landscape composition in the vicinity of focus areas has a strong influence on vegetation development (Cadavid-Florez et al., 2019; Reis et al., 2022). Our study has clearly shown that even scattered woody patches have a significant effect on mitigating the impact of climate extremes, maybe via other effects, e.g. via belowground connection among individuals via fungal species (Netherway and Bahram, 2024).

While the effect of native woody patches in the landscape dominated by grassland has already remained largely unexplored, examples are even scarcer, where the interaction of these two (i.e. woody patches and small-scale landscape features like slope and aspect) were also considered. There are only a few studies, where microtopography and woody patches (tree islands) were simultaneously considered in modulating ecological conditions (Holtmeier and Broll, 1992; Ludwig et al., 2005). They found an interplay of woody cover and microtopography in soil development with ecological significance. Our results join these findings by underlining the significance of the interplay of microtopography and presence of woody patches in the landscape - an aspect rarely considered yet, but potentially significant in the face of the expected increase in extreme drought events. In the contemporary societal context, biomass and particularly woody biomass is considered a prominent means of climate change mitigation (Domke et al., 2020; Hardaker et al., 2022; Kirschbaum et al., 2024). However, several studies indicate that fine-tuning of tree-planting is necessary to make it an effective way of mitigation (Fleischman et al., 2020; Hermoso et al., 2021; Kirschbaum et al., 2024). Our study has a particular implication in this context, not yet explored: that positioning of woody patches in a restoration or tree planting campaign can highly enhance the effectiveness of the efforts.

#### 4.2. Factors affecting the seedling cover

The emergence of perennial grass seedlings is a crucial and rare event in grassland, which could determine the recovery of this habitat after severe disturbance (Orbán et al., 2023). In our case grass seedling emergence was determined in a distinctly different pattern compared to grass dieback after the extreme event. As opposed to the case of grass dieback, the presence of woody species did not influence the pattern of seedling emergence at all. Direct shading and proximity of woody exemplars can facilitate germination of grassland species (Withgott, 2000; Gómez-Aparicio et al., 2004; Ren et al., 2008), however it is more general that increased light penetration supports the germination of open grassland species (Jutila and Grace, 2002). We examined the effect of woody patches in the broader vicinity (10 m buffer). Either, this longer-distance cover did not influence the germination of grasses or there were contradicting processes in the background and the two processes neutralised each other (Spasojevic and Suding, 2012).

On the other hand, microtopography did influence seedling emergence. Seedling emergence was lowest in north-northeastern slopes, which contradicts expectations based on relative soil water contents. In our case, however, the pattern was the opposite, which is likely in connection with the ratio of surviving and dead grass. Grass dieback was more severe in southern slopes in our study, thus creating space for germination and allowing the penetration of light onto the surface. *Festuca* species are known to germinate well in direct sunlight (Vivanco et al., 2021), thus this result is in good accordance with previous knowledge. Furthermore, Hungarian *Festuca* species were found to germinate best on plant material on the ground, i.e. plant litter or mosses (Szabó-Szöllösi et al., 2024). In concert with this, Sztár et al. (2016) found a reduced number of *Festuca vaginata* seedlings in litter removal treatment. For the other dominant grass, for *Stipa* species similar to *S. borystenica*, direct light was not found beneficial, however, shallow burial depth (1–2 cm) or shading was. The dead grass layer may exhibit the necessary burial or shading required for the germination of this species (Krichen et al., 2017; Orbán et al., 2023). Thus, the positive effect of southern slopes on germination can be explained by the presence of the dead grass layer and the absence of competition by adult grass individuals.

Also, mild slopes provided more opportunities for seedling emergence as indicated by a negative influence of slope steepness on seedling cover. This is likely due to mild slopes exhibiting less harsh environments and higher soil water content than steep slopes (Zang et al., 2020).

#### 4.3. Applicability of the results

Our results have several management implications, particularly regarding the management of woody patches in grassland matrix. Our findings showed the important effect of large shrubs or woody vegetation of even a few metres high on grassland survival. According to other studies, these do not lower the diversity of grassland species either (Paesel et al., 2019; Teleki et al., 2020; Zehnder et al., 2020). Thus, we think that the preservation or even restoration of such patches should be promoted (Tölgyesi et al., 2018; Lőrincz et al., 2024; Tölgyesi et al., 2023). Such considerations could be beneficial for conservation actions and in restoration plans to prepare for climate change effects also. Habitat restoration by shrub or wood removal is a frequent practice in Central Europe (e.g. Michielsen et al., 2017; Görzen et al., 2019; Vörös et al., 2025). Besides sustainability issues against shrub or wood regrowth detailed in Vörös et al. (2025), our study also shows that resistance against climate events might also be weakened if woody patches are automatically regarded as subject to removal. Rather woody patches should be viewed as a form of microrefugia supporting survival under climate change (Dobrowski, 2011; Gallé et al. 2024), similarly to certain landforms at a different scale, such as dolines (Bátori et al., 2021; Nadeau et al., 2022; Pastore et al., 2022) or water bodies (McLaughlin and Zavaleta, 2012). Our study has shown that the presence of woody patches has a particular significance in the face of climate change as extreme events are expected to become more common (IPCC, 2021). Extreme droughts are expected to become more frequent in central Hungary in particular (Kis et al., 2023), which calls for considerations to consider strategies to mitigate their effects on vegetation of conservation significance. Furthermore, our results also provide guidance to climate change mitigation by tree planting often endorsed by the public (Domke et al., 2020; Hardaker et al., 2022; Kirschbaum et al., 2024) itself, in the sense that it draws attention to the significance of positioning tree patches in a not fully forested landscape.

While our study highlights important relationships not identified yet, such as the interaction of microtopography and woody cover in mitigating the effects of extreme drought, it also bears limitations regarding conclusions to be drawn. One of the limitations is the single location. The relevance of results for nature conservation underlines the significance for collection of similar situations to prove our conclusions. At the same time, our case also underlines that long-term monitoring systems have scientific benefits and relevance beyond the original monitoring purpose, thanks to the coherent long-term data series they provide (Rees et al., 2001; Knapp et al., 2012; Taig-Johnston et al., 2017).

Due to the nature of the found experiment, the analysis was done in a framework designed for monitoring (Knapp et al., 2012), rather than the detection of factors influencing resistance to climate change. However, our findings have the potential to draw attention to the observed phenomenon and to motivate designing more focused field studies or even experiments in more replications.

#### 5. Conclusion

We conclude that topographic heterogeneity and presence of woody patches in the landscape contribute to the survival of dominant species of open sandy grasslands under extreme drought. Steep slopes, northern aspect or even small patches of woody vegetation can provide microrefugia where dominant grass species can endure extreme weather events, the frequency of which is expected to increase in the near future. Furthermore, we identified that microtopography and woody vegetation patches act in interaction and thus need to be considered together, when aiming at understanding and conserving dryland ecosystems. This underscores the significance of landscape heterogeneity for the persistence of grasslands in the context of the changing climate. Consequently, also bears a strong message to conservation and restoration planning by underlining the significance of allowing for grass-woodland heterogeneity even in a predominantly herbaceous ecosystem.

#### CRediT authorship contribution statement

TR and GyKD designed the monitoring. ACs, ACsCs, MH, MK, GyKD, AFN, GÓ, NS, MV conducted the field survey. GSz and LB conducted the aerial survey. AGy conducted the analysis. AGy, IS and ACs wrote the article and all authors reviewed and commented on the manuscript.

#### Ethics

Not applicable: This manuscript does not include human or animal research

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## 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 A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2025.e03596](https://doi.org/10.1016/j.gecco.2025.e03596).

## Data availability

Data will be made available on request.

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