



Linking environmental heterogeneity and plant diversity: The ecological role of small natural features in homogeneous landscapes



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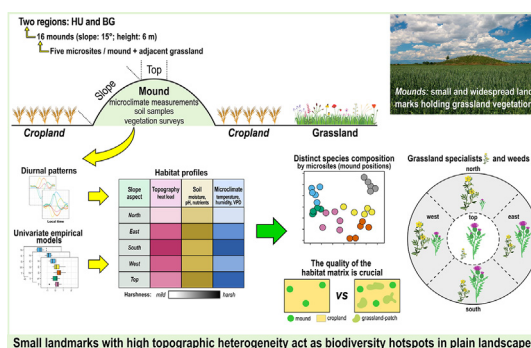
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HIGHLIGHTS

- We studied few-metres-high wide-spread landmarks in two biogeographical regions.
- We linked patterns of topography, soil and microclimate with plant biodiversity.
- We distinguished microhabitat profiles based on high-resolution measurements.
- Microhabitats had distinct species composition and harboured indicator species.
- Topographically heterogeneous landmarks act as biodiversity hotspots in plain areas.

GRAPHICAL ABSTRACT



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ABSTRACT

Small natural features (SNFs), such as road verges, midfield islets, rocky outcrops and ancient burial mounds, provide safe havens for species of natural habitats in human-modified landscapes; therefore, their great ecological importance is in contrast to their small size. SNFs often have a high topographical heterogeneity and abiotic conditions, which differ from their surroundings; therefore, they provide a unique opportunity for establishing links between environmental heterogeneity (EH) and biodiversity. However, no study has so far investigated the EH components of topographically heterogeneous SNFs in a comprehensive framework, by linking environmental and biotic parameters. To fill this knowledge gap, we evaluated the EH components and their effect on biodiversity on ancient mounds covered by semi-natural grasslands in the Pannonian (Hungary) and Continental (Bulgaria) biogeographical regions. We designated 16 study sites, each containing a few-metre-high mounds with five microsites (top, north-, east-, south- and west-facing slopes) and a nearby plain grassland. At each microsite, we measured soil moisture, soil chemical properties, solar radiation and microclimate; and recorded the cover of vascular plants in a total of 480 plots. On the mounds, topographical heterogeneity was associated with sharp differences in microclimate and soil properties. Besides the contrast between mild north-facing and harsh south-facing slopes, east- and west-facing slopes also sustained unique microsites characterised by dynamic diurnal changes in air temperature and vapour pressure deficit. Various combinations of the EH

Abbreviations: EH, environmental heterogeneity; HL, heat load; RH, relative humidity; SNF, small natural feature; SOC, soil organic carbon content; T, air temperature; VPD, vapour pressure deficit; SMC, soil volumetric moisture content.

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components resulted in unique plant species compositions within the microsites, and supported the co-occurrence of species typical of contrasting habitat types, even within a couple of metres. By combining high-resolution measurements of abiotic factors with fine-scale vegetation sampling, our study provides evidence that widespread SNFs with complex topography harbour several grassland-specialist plant species and introduce a high level of EH to otherwise homogeneous plain landscapes, which cover one third of the global land area.

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1. Introduction

Environmental heterogeneity (EH), encompassing spatial and temporal heterogeneity in biotic and abiotic factors, is considered one of the most important drivers of species richness patterns from local to continental scales (Stein et al., 2014; Tamme et al., 2010). EH is a general term used to describe the number and breadth of environmental gradients, the variety of contrasting microsites, the structural complexity and availability of resources and limiting factors within a given site (Lundholm, 2009). Overall, an increase in EH leads to niche diversification, which supports the co-existence of species specialized in particular resource regimes or combinations of abiotic factors (Tamme et al., 2010). The conservation importance of EH is being recognised globally, due to the generally positive relationships between EH and biodiversity (Báldi, 2008; Stein et al., 2014).

According to Stein et al. (2014), EH measures consist of five categories, divided into biotic (land cover, vegetation) and abiotic (climate, soil and topography) components. Land cover EH expresses the level of habitat heterogeneity within a certain site; its value increases with the number of habitat types and patches present. Vegetation EH refers to the structure of vegetation, and also to its taxonomical or functional composition. Climatic and soil EH refer to heterogeneity in micro- and macroclimatic and soil parameters. Topographic EH might refer to small-scale unevenness on the surface such as tussocks, or to large geographic formations such as mountains. Although the effects of EH components are often interrelated and all of them affect biodiversity patterns, most studies consider one, or a few, of them. Moreover, studies generally focus either on a continental/landscape-scale or a fine-scale of a few centimetres/metres, but there are only a few studies concentrating on intermediate spatial scales (Stein et al., 2014).

For establishing links between EH components and biodiversity at intermediate scales of a couple of metres, small natural features (SNFs) provide an outstanding opportunity. SNFs, such as field margins, road verges, midfield islets, stone walls, karst dolines, ancient earthworks and burial mounds can be regarded as distinct entities differing from their surroundings in their abiotic and biotic conditions, and often characterised by a high level of EH (Deák et al., 2016; Hunter et al., 2017; Lisetskii and Pichura, 2020). SNFs often provide safe havens for plant and animal species of natural habitats, even in human-modified landscapes; therefore, their great ecological importance is in contrast to their small size (Hunter et al., 2017). Besides mitigating the negative effects of habitat loss and fragmentation, some SNFs with specific microclimates (different from their surroundings) can also buffer the negative effects of climate change, which especially affects the habitat specific species pool of many vanishing natural habitats (Keppel et al., 2012; Bátori et al., 2019). Since one of the most severe habitat losses has occurred in Palaearctic temperate dry grasslands, where approximately 60% of the natural stands have been destroyed, SNFs preserving remnant grassland fragments are priority objects for conservation (Wesche et al., 2016; Biró et al., 2018). Despite the fact that SNFs are typical elements of many landscapes only a little is known about the relationship between EH components and the associated biodiversity patterns found on them.

For linking components of EH to plant biodiversity patterns on topographically heterogeneous SNFs, ancient earthen burial mounds holding millennia-old grassland habitats offer a unique study setting. In continental parts of Eurasia approximately half a million mounds dating back to

the Bronze and Iron Ages still remain in a relatively undisturbed state; therefore, despite their small size (0.1–1 ha area, 0.5–15 m height) they often act as refuge for dry grassland species, even in heavily transformed lowland landscapes (Deák et al., 2016; Dembicz et al., 2018). The refuge role of mounds is supported by their dome shape and steep slopes, which often prevent ploughing. Similarly to old cemeteries and graveyards, social taboos related to cultural heritage also contribute to the preservation of the mounds' integrity (Sudnik-Wójcikowska and Moysiyanenko, 2008; Deák et al., 2016; Löki et al., 2020). Although the conservation role of burial mounds has mainly been studied in the continental regions of Eurasia (Deák et al., 2016; Dembicz et al., 2018), ancient burial mounds are also present in high numbers in boreal Atlantic and Mediterranean Europe and in many parts of North and South America (Andrews and Fernandez-Jalvo, 2012), which might in turn further extend the geographical range of their conservation relevance.

Analogous to other features, either natural (e.g. dolines – Bátori et al., 2020a; rocky outcrops – Speziale and Ezcurra, 2014; inselbergs – Yates et al., 2019) or anthropogenic (dams – Bátori et al., 2020b; earthworks – Lisetskii and Pichura, 2020), which are characterised by higher topographical heterogeneity than the adjoining matrix, topography and topography-driven environmental conditions on mounds might strongly affect the environmental conditions, and thus vegetation patterns. Previous studies have described differences in some abiotic environmental factors and vegetation patterns in microsites within the mounds. Using the data from four Ukrainian mounds, Lisetskii et al. (2014) reported differences between the soil properties of the north-facing and south-facing slopes. Sudnik-Wójcikowska and Moysiyanenko (2008) and Deák et al. (2017) noted that the north- and south-facing slopes of mounds had a different vegetation composition both in Ukraine and Kazakhstan. However, to our knowledge no previous study has investigated the EH components on mounds, or other topographically heterogeneous SNFs in a comprehensive framework, by linking environmental and biotic parameters.

To fill this knowledge gap, here we focus on all components of EH that are potential drivers of vegetation patterns, and can contribute to the maintenance of grassland biodiversity on topographically heterogeneous SNFs. For this study, we used mounds which act as habitat islands in the Pannonian (Hungary) and Continental (Bulgaria) biogeographical regions of Europe, in order to test whether the effects of EH on vegetation composition depends on the biogeographical region. In order to understand the interactions between EH components and reveal their effects on plant diversity and species composition, we studied the five main EH components on mounds using nearby plain grasslands as a reference. On each mound, we investigated five mound microsites (slopes with different main aspects and top). Linking EH with plant diversity in these microsites may provide new insights on topographically-driven abiotic and biotic patterns at the least studied intermediate scales which are represented by a wide range of landforms globally. The majority of previous studies on topography-driven biodiversity patterns focus only on the north- and south-facing slopes, but we complemented our design by also including the east- and west-facing slopes in our study.

We asked the following questions: (i) How do microsites (top, and north-, east-, south- and west-facing slopes vs. plain grassland) contribute to the components of environmental heterogeneity? (ii) Which combinations of abiotic environmental factors characterise the microsite types studied? (iii) Do the microsites have vegetation with different species

composition; thus, can they be considered microhabitats? (iv) Are there any differences in the conservation values of the microsites in terms of the abundance and diversity of grassland specialist, generalist and weed species? We also aimed to test whether EH-driven vegetation patterns on mounds are different among different biogeographical regions and landscapes. By answering these questions, we aim to evaluate the role of SNFs with high environmental heterogeneity as biodiversity hotspots for grassland specialist species in agricultural landscapes.

2. Methods

2.1. Study sites

Our study sites are located in the Pannonian (East-Hungary) and Continental (South-Bulgaria) biogeographical regions of Europe (Fig. 1). They are situated in lowlands with open landscape structure transformed by agricultural activities. Both areas harbour a high number of well-preserved mounds built during the Bronze (Yamnaya Culture) or Iron (Thracian) Ages. The Hungarian study area situated in the Great Hungarian Plain covers an area of approximately 1406 km². This region represents a typical transformed landscape, where grassland habitats have suffered a considerable loss, but their fragments are still present (cover of semi-natural grasslands is 29% according to the Corine Land Cover database; EEA, 2018). The Bulgarian study sites are situated in the Thracian Plain and cover approximately 1093 km². This region represents a typical cleared landscape where the majority of grasslands has been lost (cover of semi-natural grasslands is 3%). Both regions are characterised by a continental macroclimate. In Hungary, the mean annual precipitation is 532 mm and the mean annual temperature is 10.2 °C; in Bulgaria, the mean annual precipitation is 533 mm and the mean annual temperature is 12.1 °C; here, the climate has a sub-Mediterranean influence (Fick and Hijmans, 2017).

In the Hungarian study region, the historical landscape was characterised by forest steppe vegetation consisting of a mosaic of extended dry grassland habitats formed on chernosemic and alkaline soils, and patches of forest stands dominated by *Quercus*, *Acer* and *Populus* species (Biró et al., 2018). Due to the agricultural intensification, which has accelerated since the 19th century, a great proportion of the natural habitats have been transformed into arable lands and urban areas. As a consequence, these habitats have suffered a considerable loss and became fragmented, especially grasslands formed on fertile

soils (Deák et al., 2020a, 2020b). Nowadays plain grasslands are generally managed by grazing or mowing.

Although the historical landscape in the Bulgarian study region was predominantly characterised by *Quercus* forests mixed with *Ulmus*, *Fraxinus* and *Acer* spp., patches of forest steppes and an extended network of dry steppe grasslands were also present (Magyari et al., 2008). Natural grasslands were mostly formed in areas characterised by alkaline soils, and on the shallow soils of slopes in the foothill regions of the surrounding mountain ranges. Landscape transformation by deforestation started in approximately 4000 BCE and likely contributed to the extension of the already existing dry grassland habitats. The human impact on the environment became stronger in the following millennia, when considerable amounts of forest and grassland habitats were transformed into ploughlands (Connor et al., 2013). Currently plain grasslands include both overgrazed and abandoned stands.

In both study regions, we selected eight sites, including one mound that has dry grassland vegetation, and the closest plain dry grassland stand representative for the study site (Fig. 1). For our study we selected a uniform set of mounds with similar shapes, landscape contexts, levels of disturbance and management in order to control for the effects of these factors and focus only on our study questions related to EH and biodiversity. The mean height of the mounds was 5.1 m (SD = 2.0) metres in Hungary and 6.5 m (SD = 3.5) in Bulgaria, the mean surface area was 3777 m² (SD = 1665) in Hungary and 3196 m² (SD = 2138) in Bulgaria, and the mean slope angle was 12.0° (SD = 2.9) in Hungary and 16.4° (SD = 4.4) degrees in Bulgaria. All selected mounds were predominantly surrounded by arable lands and forest plantations which are inadequate for the establishment of grassland species. They contained a low cover (<5%) of woody vegetation, were not affected by any human disturbances (i.e. the presence of roads, buildings and ploughing) and were unmanaged.

2.2. Field survey

We studied the five main EH components that might influence plant diversity and species composition (Table 1). For this we measured microclimate variables and in situ soil moisture content, took soil samples for chemical analyses and recorded the list and cover of vascular plants in five mound microsites (N, E, S, W-facing slopes and top) and in the nearby plain grasslands, at each study site (Fig. 2). The survey was performed in May–June 2019, as this is the best period for recording the highest

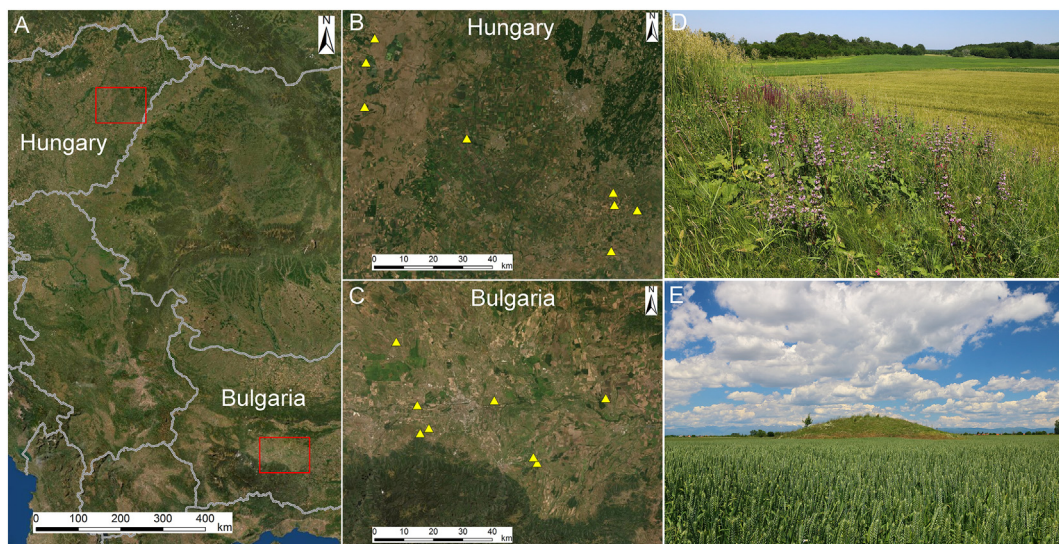


Fig. 1. Map of the studied regions and the surveyed mounds. (A) study areas; (B) map of Hungarian mounds; (C) map of Bulgarian mounds; (D) Sóllyom-mound (HU); (E) Dinkodja-mound (BG).

Table 1
The EH components and variables studied (after Stein et al., 2014).

EH component	Studied variables
Land cover	Microsites with a distinct vegetation within the mound
Vegetation	Plant cover and species density
Climatic	Heat load index, air temperature, relative air humidity, vapour pressure deficit
Soil	Moisture, pH, SOC, plant available P ₂ O ₅ , and NO ₃ ⁻
Topographic	Slopes with different aspects and the top of the mound

number of occurring plant species: both the spring annuals and the later appearing perennial species can be observed and they have the appropriate diagnostic features for identification. In each microsite, we recorded air temperature (T; °C) and relative humidity (RH; %) at 1 min intervals for 24 h (from 0:00 to 24:00, local time) using Optin Ambient TH1-32 data loggers (6 measurements/site). All loggers were equipped with a passively ventilated shading panel to avoid direct sunlight; the sensors were mounted 10 cm above the soil surface and they were located on the midpoint of the slopes and at centre of the top and in the central part of the plain grassland stand in order to have a standard position regardless of the small variation in mound sizes. We measured the soil volumetric moisture content (SMC; %) of the upper 12 cm of the soil at ten random points in each microsite using a FieldScout TDR 350 soil moisture

meter (60 measurements/site). We took soil samples using a 20 cm × 5 cm × 5 cm-sized metal core from the upper 20 cm of the soil at four random points in each microsite (24 samples/site). Soil samples from the same microsite were homogenised and then soil chemical properties (pH, soil organic carbon content (SOC), and the amount of plant available phosphorus (P₂O₅) and nitrogen (NO₃⁻)) were analysed in an accredited laboratory (NAT-1-1654/2011). In each microsite, the species list and the percentage cover of vascular plants were recorded in five randomly placed 1 m × 1 m plots (1 mound × 5 microsites × 5 plots + 1 plain grassland × 5 plots = 30 plots per site). In total, we sampled 2 regions × 8 sites × 30 plots = 480 plots.

2.3. Data processing

2.3.1. Abiotic environmental data

For estimating the amount of solar radiation received by a certain microsite we calculated the heat load index, which is a combined measure of latitude, slope and aspect. For calculating heat load (HL), we applied the equations based on least-squares multiple regression using trigonometric functions of latitude, slope and aspect, as suggested by McCune and Keon (2002). We calculated vapour pressure deficit (VPD) values which characterizes the actual drying capacity of air from air temperature (T) and relative humidity (RH) data (Allen et al., 1998). For the interpretation of diurnal cycles focusing on the daily

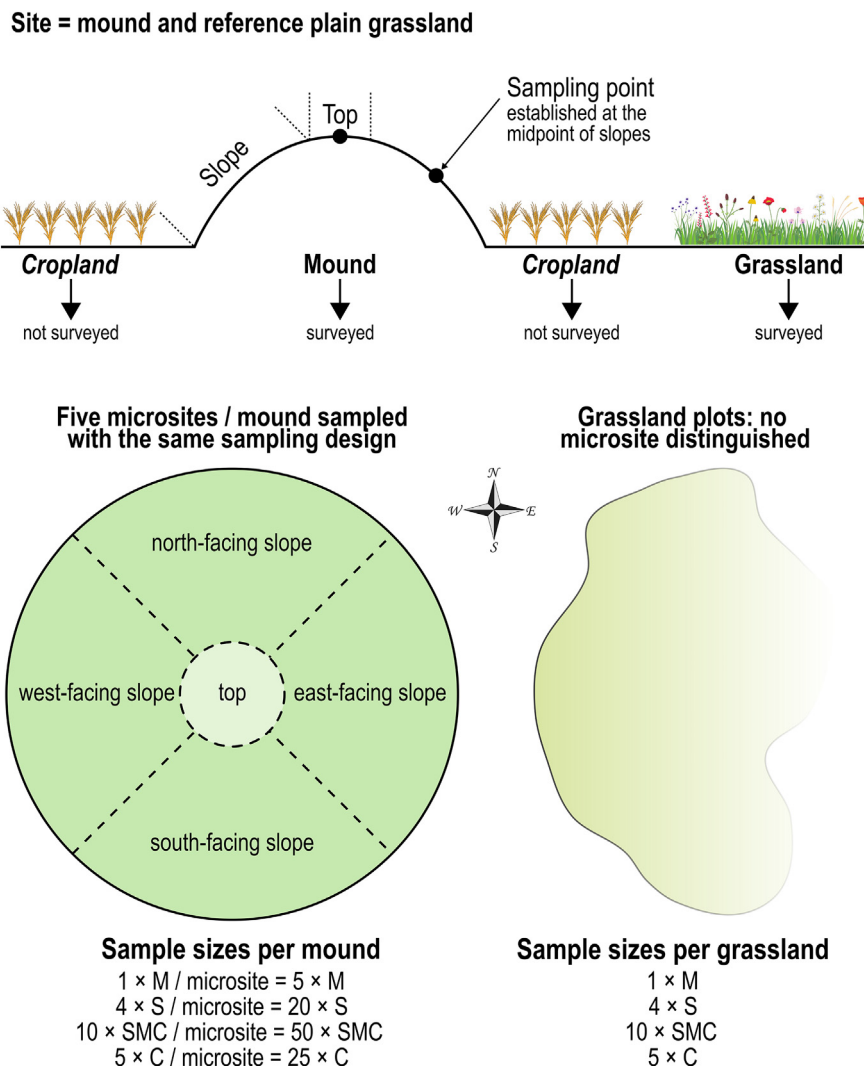


Fig. 2. The sampling design applied. Plant element vectors are licensed by Freepik (<http://www.freepik.com>). Notations: M – microclimate measurements (air temperature, relative humidity); S – soil samples (pH, SOC, amount of plant available P₂O₅ and NO₃⁻); SMC – volumetric moisture content of the soil; C – coenological relevés (species occurrence and cover data).

changes in T, RH and VPD, we plotted microclimate variables using local regression models (LOESS smoothers) on the observed data (Zuur et al., 2009). For exploring the differences in the abiotic characteristics between mound microsites, we calculated the relative values of heat load (ΔHL), microclimatic (daily means of ΔT , ΔRH , ΔVPD) and soil

(ΔpH , ΔSOC , ΔP_2O_5 , and ΔNO_3^- , ΔSMC) parameters. Specifically, relative mean values per microsite were calculated as differences from the values measured in the corresponding plain grassland microsite. By using relative values, we were able to properly test the differences in the abiotic environmental parameters between mound microsites.

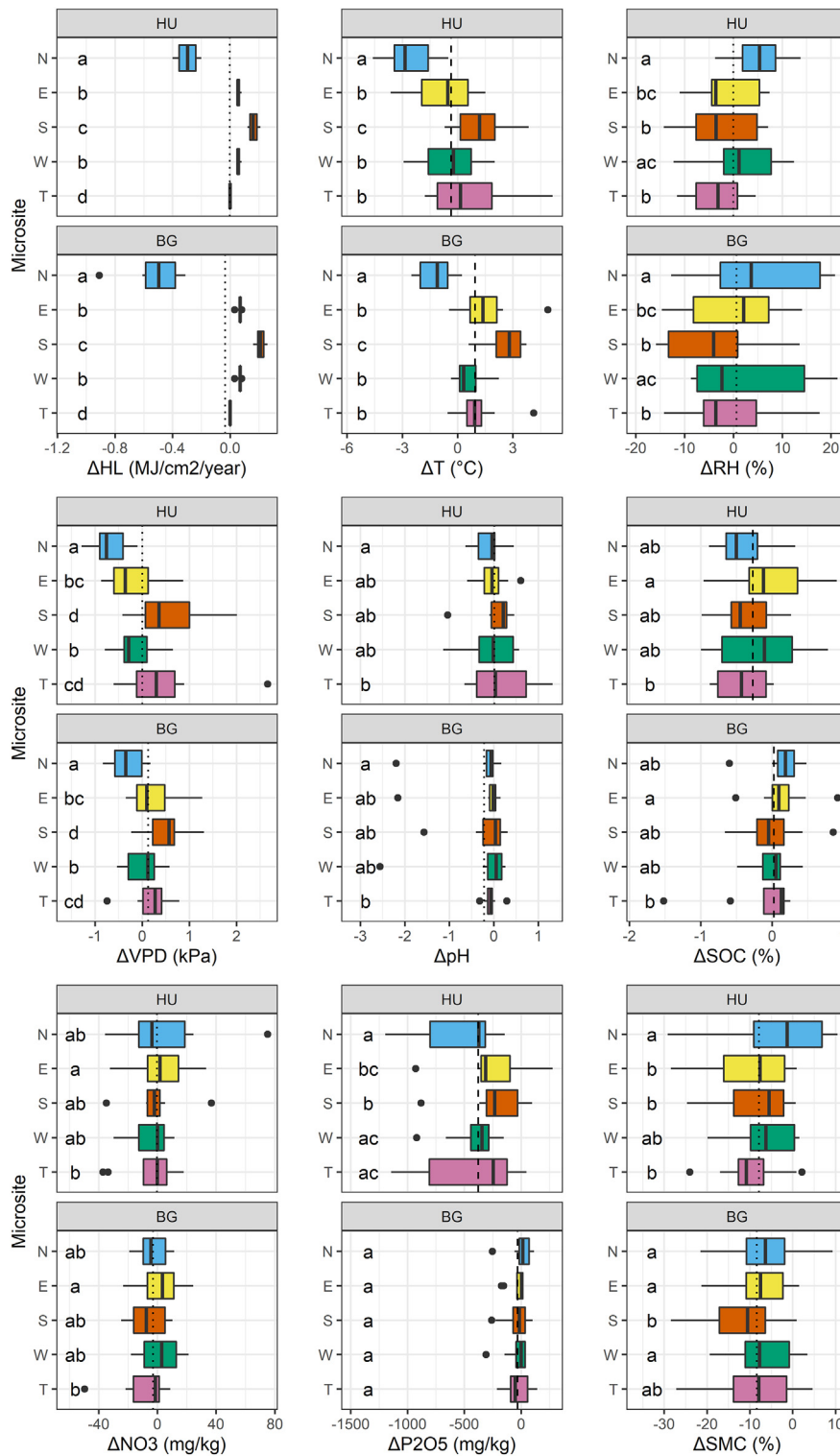


Fig. 3. Relative values of abiotic data measured in the five mound microsites in Hungary (HU) and Bulgaria (BG). Relative values were calculated as the differences from the values measured in the adjoining plain grassland. Boxes represent the interquartile region of value distribution (between 25% and 75% quartiles), the bold inner lines visualize the median, the horizontal lines show the value range from minimum to maximum values, and separate dots represent outliers (values that are lower or higher by 1.5× the interquartile range from the lower or upper quartile, respectively). Notations: dotted line – mean of the measured values without significant differences between regions; dashed line – mean of the measured values with a significant difference between regions. Letters denote significant differences between groups, assessed separately for regions (from models fitted with MCMCgmm). For the minimum, maximum and mean values of the measured abiotic environmental data, please see Table S2.

2.3.2. Vegetation data

We classified the species according to their habitat preferences using the descriptions and classifications of Borhidi (1995) (Hungary) and Delipavlov et al. (2011) (Bulgaria). Species occurring exclusively in dry grassland habitats were considered dry grassland specialists, species typical of disturbed habitats were considered weeds, and all other species were considered generalists (hereafter specialists, weeds and generalists). By using indicator species analysis, we also determined species that are ecological indicators of certain habitat types and environmental conditions related to the habitats (Cáceres and Legendre, 2009). Plant nomenclature follows The Plant List (2017).

2.3.3. Statistical analyses

We used R (version 3.6.3, Team R Core, 2020) for all statistical data analyses. For testing the effects of the region (Hungary, Bulgaria) and mound microsites (four slopes and top) on the relative values of abiotic environmental parameters (Δ HL, Δ T, Δ RH, Δ VPD, Δ pH, Δ SOC, Δ P₂O₅, and Δ NO₃⁻, Δ SMC), we fitted mixed-effects linear regression models (LMMs) separately for all abiotic environmental parameters (using them as response variables), with microsite and region as predictors, also controlling for their interaction. We specified site ID as a random effect to control for spatial autocorrelation in the data. To fit models, we used the R-package “MCMCglmm” using a Markov chain Monte Carlo (MCMC) approach in a Bayesian framework (Hadfield, 2010), because it not only allows for simple specification of random effects, but also allows the use of an inverse distance matrix of the random groups (proportional to the covariance structure of random effects): this approach provides a method to control for spatial autocorrelation in the data. In order to aid model fitting, we re-scaled response variables by subtracting the variable mean from all values in the given variable, and dividing by one standard variation. For model fitting, we used weakly informative, proper priors (i.e. prior distributions that did not considerably constrain the sampled posterior distribution, and prior distributions that integrate to one), and also parameter expanded priors for the random effects to aid MCMC chain mixing throughout model fitting. To give the sampling algorithm sufficient time to converge and adequately sample the posterior distribution of parameter estimates, we ran MCMC chains for 105,000 iterations, from which the first 5000 were discarded as “burn-in”, and only every 50th iterations was saved, yielding posterior distributions with a nominal sample size of 2000. We carried out model diagnostics by using the package “coda” (Plummer et al., 2006) to quantify autocorrelation within MCMC chains: we considered chains to have been mixing well when the absolute value of autocorrelation within chains was <0.1. This criterion was met by all MCMC chains in the models reported in the results. To establish statistical significance, we assessed the 95% highest posterior density (HPD) interval of parameter posterior distributions: we considered parameter estimates to be significant when HPD intervals did not cross zero. To quantify grouping factor level contrasts, we extracted estimated marginal means with the R-package “emmeans” (Lenth, 2019).

We excluded non-significant interaction terms between the fixed predictors (i.e. when microsite effects did not differ across regions) from the final models.

For testing differences in vegetation components, LMMs were fitted with “MCMCglmm”, in which we included region, microhabitat, and their interaction term as fixed predictors. Response variables were total species density (i.e. the number of species in the 1-m² plots), total vegetation cover, and, separately, the species density and cover of specialist, generalist, and weed species. Prior to model fitting, species coverage data of generalists and weeds were log-transformed to normalize distribution and improve model fit. Similarly to the previously described MCMCglmm models, site ID was specified as a random factor, and the inverse distance matrix of sites was used to approximate the covariance structure of random effects.

We applied non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA with 999 permutations) using the Bray-Curtis index of dissimilarity to test differences in the species composition among microhabitats in the two studied regions and in the individual sites separately. Rare species (occurrence at ≤5% of the total plot number) were excluded from the analyses. NMDSs and PERMANOVAs were performed using the “vegan” package (Oksanen et al., 2019). For the indicator species analysis, we applied multi-level pattern analysis using the “indicpecies” package (Cáceres and Legendre, 2009).

3. Results

3.1. Abiotic environment

Δ HL was the highest on south-facing and the lowest on north-facing slopes (Fig. 3; Table S1). Values on the top were comparable to those in the reference (i.e. neighbouring grasslands). The HL received by west and east-facing slopes did not differ, and were intermediate. Δ T was significantly lower in Hungary than in Bulgaria. It was the highest on the south-facing slopes and top, represented by predominantly positive relative values, whereas it was the lowest on the north-facing slopes represented by negative values. Δ RH was the highest on the north-facing slopes, and lowest on the south-facing slopes and top in both regions. Δ VPD showed the opposite pattern. Δ pH was the lowest on the north-facing slopes (although it differed significantly only from the top). Δ SOC and Δ NO₃⁻ were the highest on the east-facing slopes. We observed significantly higher SOC values in Bulgaria than in Hungary. We did not find any significant regional differences in the mean of Δ RH, Δ VPD, Δ pH and Δ NO₃⁻ values. Δ P₂O₅ was the lowest on the north-facing, and the highest on the south-facing slopes of Hungarian mounds. We observed no significant differences between microsites in the case of Bulgarian mounds. Δ SMC scores were all negative; thus, SOC was significantly lower on mounds than in grasslands. Δ SMC was the highest on the north-facing slopes, and lowest on south-facing

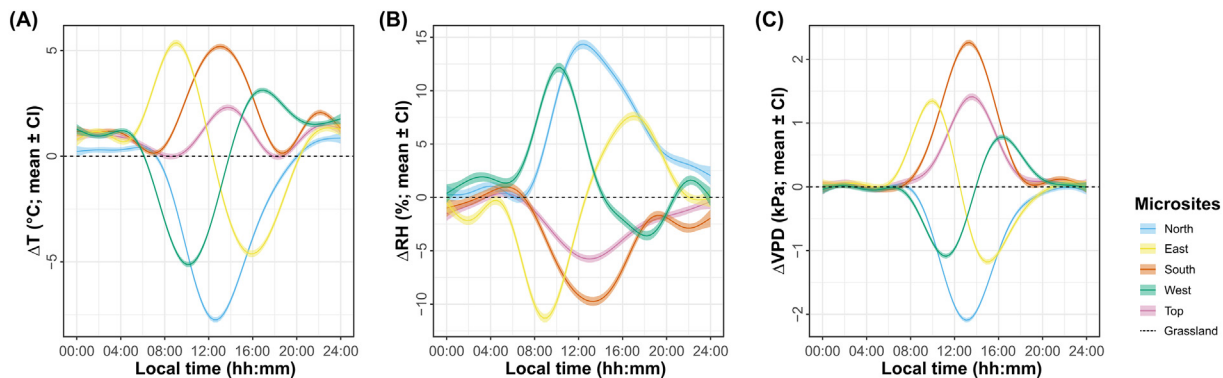


Fig. 4. Diurnal variations of (A) Δ T, (B) Δ RH and (C) Δ VPD in the studied microsites. Relative values were calculated as temporally synchronized differences from the values measured in the adjoining plain grassland. Lines represent the LOESS smoothed mean values while bands are 95% confidence intervals based on the 16 surveyed sites.

slopes. In Hungary, the ΔSMC scores of the north-facing slope were significantly higher than on the south- and east-facing slopes and top. In Bulgaria, ΔSMC scores were significantly higher on east-, west- and north-facing slopes than on south-facing slopes.

Diurnal patterns of ΔT, ΔRH and ΔVPD (Fig. 4) confirmed the mean differences in microclimatic variables among microsites (Fig. 3). Moreover, we detected large within-day variations that were most pronounced on the east-facing slopes (warm and dry morning followed by relatively cold and moist afternoon) and west-facing slopes (morning: cold and moist; afternoon: warm and dry). Peak times of maxima and minima also shifted considerably, according to the microsites; east-facing slopes became the warmest and most vapour-deficient approximately 45 min earlier than plain grassland sites; on the contrary,

west-facing slopes could retain local air humidity longer (RH_{min} had a lag of approximately 60 min) (Fig. 4; Table S3).

3.2. Vegetation

Based on the multivariate analyses (NMDSSs, PERMANOVAs), the vegetation composition of microsites showed clear patterns at the site level, but despite the significant separation, at the regional level plots representing different microsites overlapped considerably in the multivariate ordination space (Fig. 5). NMDSS ordinations (stress: 0.238 for Hungary and 0.251 for Bulgaria, respectively) revealed a relatively homogeneous group of grassland plots in both regions. Moreover, in the case of Bulgarian mounds, microsites had a more distinct species

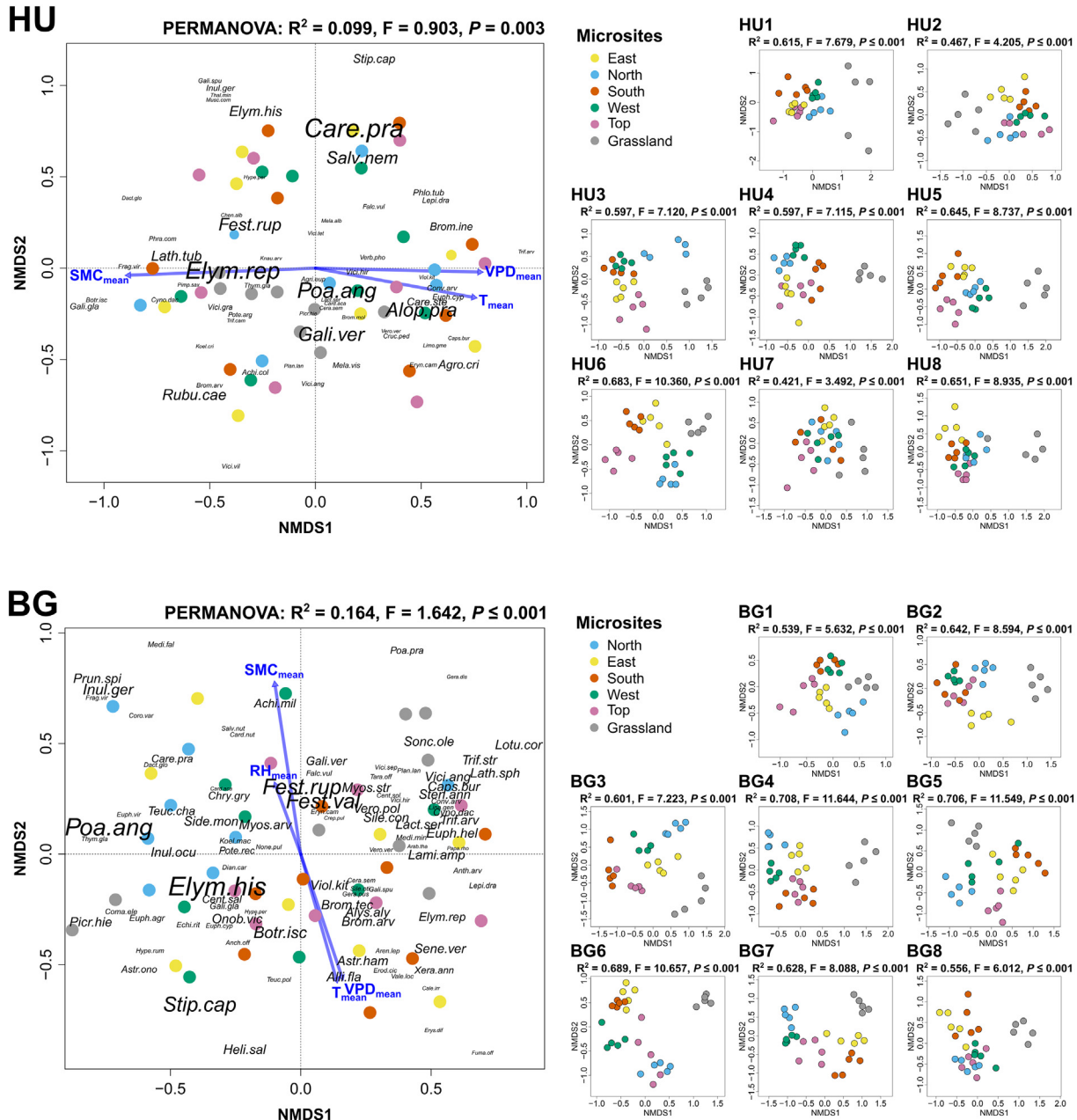


Fig. 5. Ordination diagrams from the non-metric multidimensional scaling, displaying the species compositions of the studied microsites (HU – Hungary; BG – Bulgaria). Large panels show the patterns on the regional level (points with the same colour denote the average of five plots per microsite per site), whilst small panels show the species composition of different microsites on the site level (one point represents one plot). We plotted 70% of the most frequent species on the figures (see Table S4 for full names); font size corresponds to the frequencies. Environmental variables with statistically significant ($P < 0.05$) correlations with sample scores were included as overlays onto the NMDSS diagrams: T_{mean} – mean air temperature, RH_{mean} – mean relative air humidity, VPD_{mean} – mean vapour pressure deficit, SMC_{mean} – mean soil moisture content. Results of the PERMANOVAs (coefficient of determination, F and P values) are portrayed on each graph panel.

composition compared to the Hungarian mounds. At site level, grassland plots showed the strongest separation from the other microsites. In both regions, the main gradients in vegetation composition were mostly shaped by microclimate and soil moisture; environmental gradients can be interpreted as a transition from the relatively cool and moist towards the warmer and drier microhabitats. According to the analyses, soil chemical variables were not identified as significant drivers of plant assemblages.

We recorded 304 plant species in total, including 104 grassland specialists on the study sites (Table S4). We found altogether 74 species (28 specialists) occurring only in Hungary and 137 species (55 specialists) occurring only in Bulgaria; the number of species common to both

regions was 93 (of which 21 were specialists). The number of indicator species typical of a particular microsite was 63 in Hungary and 93 in Bulgaria (Table S5). In both regions, species density in plain grasslands was higher than on any of the mound microsites separately. In Hungary, total species density was higher on north-, west- and east-facing slopes than on south-facing slopes and top, whilst in Bulgaria we detected no difference among microsites regarding total species density (Fig. 6, Table S1).

Total vegetation cover was higher in Hungary than in Bulgaria (Fig. 6, Table S1). In Hungary, the total vegetation cover was highest in north- and west-facing slopes and lowest on south-facing slopes. In Bulgaria, total vegetation cover was highest on north-facing slopes,

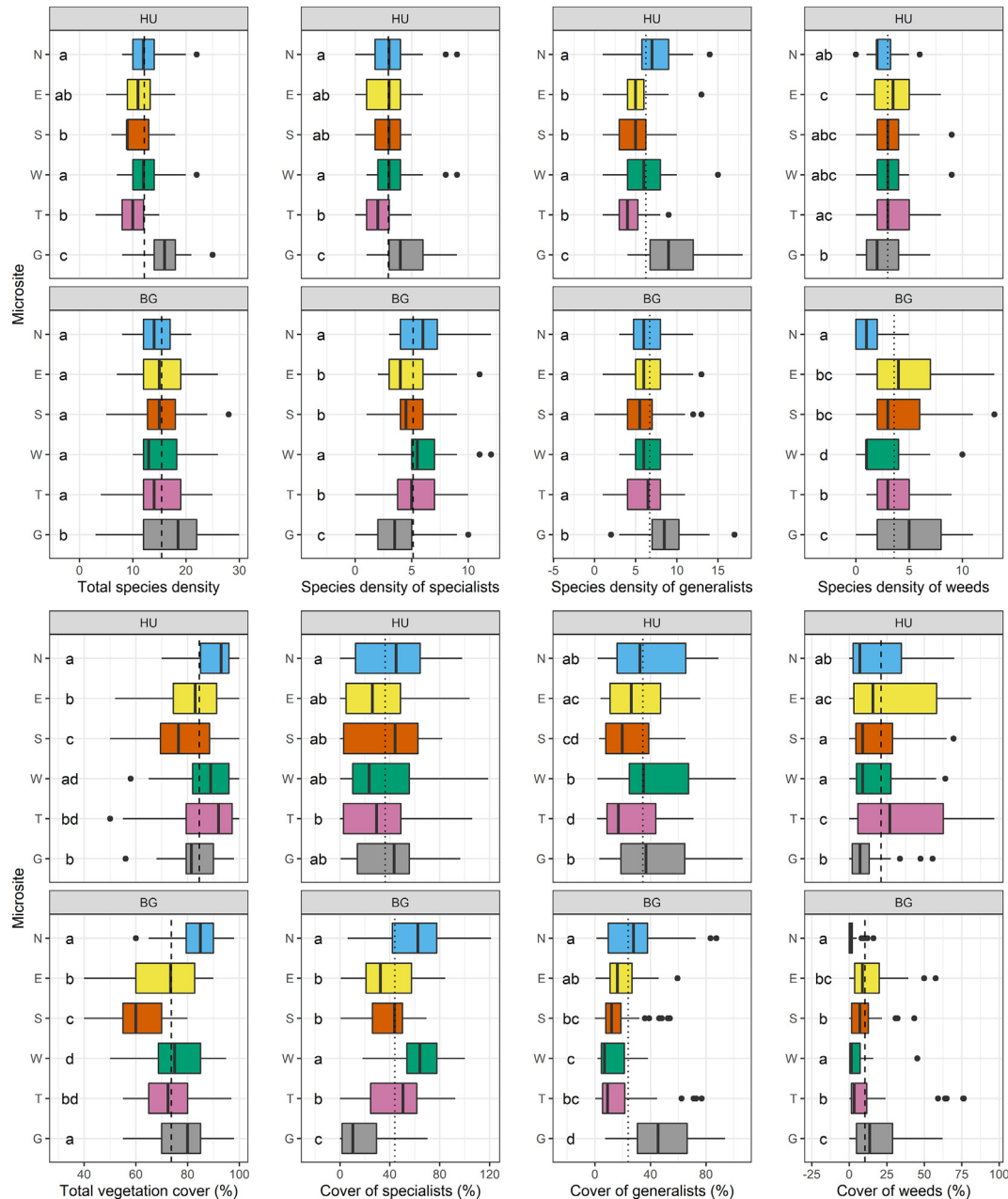


Fig. 6. Boxplots of total species density, total vegetation cover, species density and cover of specialists, generalists and weeds in the studied microsites in Hungary (HU) and Bulgaria (BG). Boxes represent the interquartile region of value distribution (between 25% and 75% quartiles), the bold inner lines visualize the median, the horizontal lines show the value range from minimum to maximum values, and separate dots represent outliers (values that are lower or higher by 1.5× the interquartile range from the lower or upper quartile, respectively). Notations: dotted line – mean of the measured values without significant difference between regions; dashed line – mean of the measured values with a significant difference between regions. Letters denote significant differences between groups, assessed separately for regions (from models fitted with MCMCglmm). For the minimum, maximum and mean values of the measured vegetation data, please see Table S6.

and exceeded the cover scores in all other mound microsites. Total vegetation cover on west- and east-facing slopes and top was higher than on south-facing slopes.

The density of specialists was significantly higher in Bulgaria than in Hungary (Fig. 6, Table S1). In Hungary, plain grasslands held the most specialists; within the mound, north- and west-facing slopes held more specialists than top. Specialist cover was higher in north-facing slopes than in top. In Bulgaria, species density and cover of specialists were lowest in plain grasslands. Within the mound, species density and cover of specialists were highest on north- and west-facing slopes, and lowest on south- and east-facing slopes and top. In Hungary, the species density of generalists was highest in plain grasslands. Within the mound habitats north- and west-facing slopes held the highest density and cover of generalists (Fig. 6). The species density and cover of generalists in Bulgaria was highest in plain grasslands. Within the mound, their cover was highest on north-facing slopes. In Hungary, the species density and cover of weeds was highest on top (Fig. 6). Their cover was lowest in plain grasslands. In Bulgaria, the species density and cover of weeds was lowest on north- and west-facing slopes and highest in grasslands.

4. Discussion

4.1. Fine-scale microsite differentiation

We observed clear general patterns regarding the fine-scale differentiation of the microsites. We could verify sharp differences in several environmental variables between north- and south-facing slopes, similarly to previous studies performed on larger scales, such as mountain ranges or karst dolines (Bátori et al., 2019; Scherrer and Körner, 2010). Besides validating the EH-driven environmental differentiation at intermediate scales, our results also highlight that east- and west-facing slopes – which have been largely neglected in previous EH studies – are characterised by unique environmental features.

4.1.1. Microclimate

In both regions, north-facing slopes received the least, and south-facing slopes the most radiation. Given their flat position, top received exactly the same amount of radiation as plain grasslands, and east and west-facing slopes received more radiation than top and plain grassland. These patterns are due to the daily orbit of the Sun and the dome shape of the mounds (Oke, 2002). It was only slightly affected by the small variation in the angle of the mound slopes, which suggests that the microclimatic patterns described can be relevant in several other types of small natural features with different slope angles. Our findings confirm the results of Lisetskii et al. (2014) on Ukrainian mounds and Bennie et al. (2006) on chalk grasslands, both reporting contrasting patterns in HL between north- and south-facing slopes. We found that the heat load received by north-facing slopes was approximately half, and by south-facing slopes double the values measured in plain grasslands, suggesting that mound microsites introduce a large heterogeneity into the otherwise plain landscape regarding HL values.

The amount and temporal dynamics of solar radiation considerably affected other microclimatic variables (e.g. daily patterns and relative means of T and VPD) and also the soil moisture of north- and south-facing slopes. Variations in radiation can considerably influence the timing of snowmelt and water runoff, which can affect both other abiotic conditions (air temperature, soil moisture) and the phenology of plants (Sudnik-Wójcikowska and Moysiyanenko, 2008; Lisetskii et al., 2014; Bátori et al., 2019; Scherrer and Körner, 2010). Although top and east and west-facing slopes received almost the same amount of intermediate level heat load, the different temporal pattern of the radiation resulted in contrasting patterns in the microclimates and soil moisture of the different microsites.

As has been found in large (mountains) and medium sized (rocky outcrops and dolines) topographic features (Bennie et al., 2008; Scherrer and Körner, 2010; Bátori et al., 2019), the north-facing slopes of the mounds were the coolest compared to all studied microsites, and south-facing slopes and top could be considered the warmest microsites. As shown by the diurnal variations, the difference between north- and south-facing slopes was greatest when the Sun is at the zenith (at about 13:00). At that time north-facing slopes were 5.1 °C cooler and south-facing slopes 7.6 °C warmer than plain grasslands. This high level of within-mound climatic variability is slightly greater than the variability observed in adjacent north- and south-facing slopes in British calcareous grasslands (range 2.5–3 °C; a difference in elevation of ten or twenty metres; Bennie et al., 2008), Patagonian rocky outcrops (range approx. 5 °C, a difference in elevation of a couple of metres; Speziale and Ezcurra, 2014) and Central-European dolines (range 8 °C; 200 m wide and 20 m deep; Bátori et al., 2019) of a larger size. The reason for the smaller between-slope differences in these habitats might be due to the milder macroclimate in regions where the studied calcareous grasslands, rocky outcrops and dolines occur, and also to the different vegetation structure of the dolines (generally covered by woody species or tall vegetation buffering contrasts in microclimates). In the case of mounds occurring in regions with a generally harsh continental macro-climate, small-scale micro-topographical differences are equivalent to large latitudinal (several hundreds of kilometres) and elevation differences (the observed 12.7 °C range in temperature within the small area of a mound is roughly equivalent to a shift of couple of hundred metres in altitude; Körner, 2007) over very short horizontal distances. The microclimatic differentiation detected on the mounds in our study highlights the importance of small landforms in plain areas that can introduce a high level of EH to the otherwise homogeneous landscape.

Although the top receives the same amount of solar radiation as plain grasslands, the high temperature values might be explained by the updraft of the hot air from the adjacent currently warming slopes. Diurnal patterns also suggest that mounds provide warmer habitat conditions compared to the plain grasslands, both in the daytime and at night. Temperature patterns significantly influenced both the RH and VPD scores. Given the lower level of evaporation, the constantly cool north-facing slopes were characterised by the highest RH and lowest VPD, while on the warm south-facing slopes we observed the opposite pattern. The largest differences in the VPD between south- (+2.3 kPa) and north-facing slopes (–2.1 kPa) were also recorded when the Sun was at the zenith.

Our study revealed that the mound microsites were characterised by considerable fluctuations between extreme positive and negative relative values of T, RH and VPD. In the morning, the air of the east-facing slopes warms up faster than the plain grassland or the top, and becomes dry, while west-facing slopes remain cool and humid. In the afternoon, this pattern reverses, but west-facing slopes dry and warm up to a lesser degree (Oke, 2002). Diurnal variations are due to the temporal changes in solar radiation received by the different microsites. East-facing slopes warms up and consequently become drier earlier than plain grasslands and other mound microsites (Oke, 2002). Besides reducing the RH and increasing the VPD, increased temperature also results in the evaporation of dew, which otherwise could be an important water source for plant species, especially under dry weather conditions, and could ameliorate the microclimate for a longer period through evaporative cooling (Agam and Berliner, 2006).

4.1.2. Soil parameters

Our results confirm the patterns described by Lisetskii et al. (2014), namely that the north-facing slopes of the mounds are affected by a higher level of leaching which results in a decrease in carbonate content and consequently in a lower pH. As was also shown by Lisetskii et al. (2014) in Ukrainian mounds, in the case of the Hungarian mounds we found low ΔP_2O_5 amounts in north-facing slopes, likely due to the

relatively moister soils, which likely support the diffusion of P into the deeper soil layers and enhance plant P_2O_5 uptake (Dunham and Nye, 1976). We found a high level of SOC content and NO_3^- in east-facing slopes. This might be due to the harsh conditions typical to eastern slopes. Under harsh conditions decomposition of plant litter is slower, which result in a continuous nutrient input compared to the other slopes where decomposition is faster; thus the availability of the released nutrients is less even (Florinsky et al., 2002).

SMC values showed that, overall, mounds were drier habitats compared to the plain grasslands. The low soil moisture in mound microsites is due to the increased distance from the groundwater, the quicker runoff of precipitation from the top and slopes, and the increased evaporation and transpiration, both resulting in drier environmental conditions (Lisetskii et al., 2014). As was described in the case of Brazilian granite inselbergs, the abovementioned effects can be enhanced by the higher chance of constant winds generally typical of elevated convex landforms (de Paula et al., 2019). The dry soil conditions and the large distance to groundwater that roots have to overarch both hinder the water uptake possibilities for plants. We observed contrasting Δ SMC values between north- and south-facing slopes. As suggested by Bennie et al. (2006) who studied chalk grasslands, this difference is primarily driven by the solar radiation received. The patterns in Δ SMC were similar to those of microclimatic parameters; however, differences in soil moisture were less pronounced and there were larger overlaps between microsites. The relatively small differences in SMC between the microsites might be due to the fact that the lateral diffusion of soil moisture, and the water uptake of vegetation can buffer the contrasts. For example, when air temperature is low, and air moisture is high on north-facing slopes, the high vegetation cover results in an increased water uptake and evapotranspiration.

We found that despite their small area, the complex topography of the mounds sustains a high diversity of microsites characterised by unique combinations of environmental conditions, and thus introduces a high level of topographical, climatic and soil EH into otherwise homogenous landscapes. Both climatic and soil EH are basically driven by the topography, especially the aspect of microsites. Our results suggest that topography has the greatest impact on microclimates by influencing the amount of radiation received. We observed marked differences between the mild north- and the harsh south-facing slopes and the top, but we also revealed a less studied pattern, namely that east- and west-facing slopes sustain unique microsites characterised by dynamic diurnal changes in T and VPD. Based on our results, north- and west-facing slopes can be regarded as mild, while east- and south-facing slopes and top as harsh microsites (Table 2). The differences observed in environmental parameters have the potential to influence the species composition of the microsites by affecting reproduction (e.g. phenology), establishment (e.g. germination, seedling establishment), physiological processes (e.g. metabolism, photosynthesis and evapotranspiration) and interspecific interactions (e.g. competition). Consequently, they can lead to the formation of distinct microhabitats (Scherrer and Körner, 2010; de Paula et al., 2019; Bátorfi et al., 2020a).

4.2. Vegetation patterns

We found that the different abiotic environmental conditions represented by microsites were reflected in the vegetation patterns; thus, the

microsites studied function as microhabitats for plant species. Differences in plant species composition and the species density of plants lead to the formation of two biotic components of EH (land cover and vegetation EH) within the mounds.

4.2.1. Species composition

On the site level we detected clear patterns in both regions; the vegetation composition of mild and harsh mound microhabitats and the grassland were well-separated in all the sixteen sites. Besides the site-level differences, in Bulgaria, our analyses revealed that even on the regional level species composition corresponded considerably to the abiotic conditions provided by the unique microsites. In Bulgaria, the mild (high RH and SMC content, and low T and VPD values) north- and west-facing slopes had similar species composition, dominated by specialists such as *Elymus hispidus*, *Stipa capillata*, *Inula germanica*, *Helianthemum salicifolium*, and *Inula oculus-christi*, and only a few species indicating degradation. This is supported by the results of the models and suggests that mild microhabitats harbour not only indicator specialist species, but also several non-indicator grassland specialists. The harsh south-facing slopes and top shared similar species composition, harbouring stress- and disturbance-tolerant generalists and weeds (e.g. *Elymus repens*, *Bromus* spp., *Senecio vernalis*). The varying but harsh east-facing slopes showed a scattered pattern. Plain grasslands were characterised by a rather distinct species pool containing mostly weeds and generalists.

4.2.2. Total cover and species density

We found a considerable contrast between the total vegetation cover in mild and harsh microhabitats in both regions, and plain grasslands had intermediate total cover scores. Mild environmental conditions typical of north- and west-facing slopes likely supported higher biomass production and vegetation cover, while harsh environmental conditions typical of south-facing slopes allowed a limited biomass production resulting in low vegetation cover (Bennie et al., 2008). Within Hungarian mounds total species density was clearly driven by the abiotic environmental factors; i.e. fewer species occurred in the harsh microhabitats. In Bulgaria total species density was similar among mound microhabitats, due to the different relative proportion of the specialist, generalist and weed species (please see below). The plain grasslands were characterised by higher species density than any of the individual mound microhabitats in both regions.

4.2.3. Specialists

We found that despite their small size, each mound microhabitat was characterised by a higher species density of specialists than that found in plain grasslands in the cleared landscapes of Bulgaria, which suggests that they act as important safe havens for grassland specialists. On the contrary, in the transformed landscapes of Hungary the species density of specialists was the highest in the plain grasslands. This contrasting pattern is likely caused by the different amount of available habitats and different types of land use. The Bulgarian cleared landscape has very few, fragmented, generally small-sized and inadequately managed plain grasslands, which leads to the reduced species density of specialists. The main reasons are the lack of meta-population connections caused by dispersal limitation among distant patches, the genetic drift of small populations, the increased level of disturbance due to intensive

Table 2

Characterisation of abiotic factors on the mound microsites, based on the results. Abbreviations: relative values of heat load (Δ H), daily mean temperature (Δ T), daily mean relative humidity (Δ RH), daily mean vapour pressure deficit (Δ VPD) and soil moisture content (Δ SMC).

Microsite	Δ H	Δ T	Daily T dynamics	Δ VPD	Daily VPD dynamics	Δ SMC	Character
North	Small	Cool	Unimodal	Humid	Unimodal	Humid	Constantly mild
South	Large	Warm	Unimodal	Dry	Unimodal	Dry	Constantly harsh
East	Moderate	Moderate	Bimodal	Moderate	Bimodal	Moderate	Varying, rather harsh
West	Moderate	Moderate	Bimodal	Moderate	Bimodal	Moderate	Varying, rather mild
Top	Moderate	Warm	Unimodal	Dry	Unimodal	Moderate	Constantly harsh

management and the invasion of generalist and weed species from the neighbouring anthropogenic habitats (Lindborg et al., 2014). Conversely, transformed landscapes in Hungary contain a considerable amount of grasslands maintaining a significant proportion of the historical species pool of specialists by providing adequate habitat conditions and functional connections between grassland stands (Biró et al., 2018; Helm et al., 2006).

We found that despite their small area (<1 ha) and isolated state, mounds still contain a large number of specialist species in both regions. This pattern is supported by the overall dry environmental conditions typical of mounds. As was shown by previous studies on dry grasslands (grassland fragments – Janišová et al., 2014; midfield islets – Lindborg et al., 2014; chalk grasslands – Bennie et al., 2006; mounds – Deák et al., 2016) low soil moisture can provide considerable support for the survival of stress-adapted dry grassland vegetation, and also enhance resistance against the encroachment of competitive, but less stress-tolerant generalists and weeds. We detected considerable differences in the cover and species density of specialist species within the mound microhabitats. Similarly to dolines (Bátori et al., 2019) and inselbergs (Yates et al., 2019), a high level of topographic heterogeneity generated a complex pattern of the abiotic conditions measured. These characteristics lead to a high environmental heterogeneity on the mounds influencing the abundance, species density and species composition of specialists. Specialist density was the highest in mild microhabitats (north- and west-facing slopes), and lowest in harsh microhabitats (south- and east-facing slopes and top). This suggests that although dry grassland specialists are adapted to high temperature, solar radiation and drought, their optimum is shifted towards milder conditions than those provided by plain grasslands under the given macroclimate. The cover of specialists showed the same pattern as their species density in Bulgaria. In Hungary, we did not observe any pattern in the cover of specialists within mound microhabitats, probably due to the slightly milder macroclimate. A high species density of specialists in mild microhabitats such as the north-facing slopes of SNFs in the northern hemisphere was also observed in dolines (Bátori et al., 2019) and mounds in Ukraine and Kazakhstan (Sudnik-Wójcikowska and Moysiyenko, 2008; Deák et al., 2017). However, our study is the first to reveal that west-facing slopes characterised by mild but varying conditions also act as important safe havens for specialists.

In both regions, we detected similar patterns in the indicator species of the particular mound microhabitats. Mild north- and mild but varying west-facing slopes predominantly harboured specialists (*Phlomis tuberosa*, *Teucrium chamaedrys* and *Trifolium alpestre*) typical of forest steppes (Borhidi, 1995). Despite the great geographical distance, mild mound microhabitats shared some common indicator herbs, such as *Filipendula vulgaris* and *Fragaria viridis* in both regions. Also, in Bulgaria, dwarf shrub species typical of the shrub layer of forest edges in forest steppe communities (*Chamaecytisus albus* and *Rosa gallica*, Borhidi, 1995, Delipavlov et al., 2011) occurred on the mild microhabitats. The harsh top and south-facing slopes and the varying east-facing slopes provided habitat for *Agropyron cristatum*, a species of Eurasian continental steppes (Wesche et al., 2016), several species typical of dry sandy and foothill grasslands (*Astragalus hamosus*, *Dianthus carthusianorum*), and also species with a sub-Mediterranean distribution area (*Convolvulus cantabrica*, *Teucrium polium*).

Our results revealed that despite the small size of the mounds, due to the high level of environmental heterogeneity, they can provide refuges for rare steppe and forest steppe specialists with contrasting habitat requirements. Many of them were indicator species of mound microhabitats and were absent from plain grasslands. North- and west-facing slopes had a mild microclimate analogous to the milder macroclimate of the forest steppe biome. East- and south-facing slopes and top had a harsh microclimate, which can be considered a fine-scale analogue of the continental steppes and Mediterranean dry grasslands. These results highlight that in both regions, the EH provided by the mounds enables the preservation and coexistence of species typical of different

biomes within a small area. As steppe and forest steppe are among the most endangered grassy biomes in the world (Wesche et al., 2016), mounds as safe havens for their characteristic species are of crucial importance for biodiversity conservation.

4.2.4. Generalists and weeds

We found that the abiotic environment was an important driver of species density and cover of both generalists and weeds. Whilst generalists preferred mild mound microhabitats and were suppressed in harsh microhabitats, weeds showed an inverse pattern. In both regions the mild microhabitats, especially the north-facing slopes, were characterised by the lowest, and the harsh microhabitats by the highest level of weed encroachment. For generalists, mounds providing overall drier soil conditions compared to the neighbouring areas can be considered suboptimal habitats, since due to environmental filtering the establishment of generalists which generally prefer mild microhabitats is hindered on the mounds. Consequently, they can only become established in mild microhabitats and are suppressed in harsh microhabitats characterised by dry soil conditions and harsh microclimates which suppress the germination and establishment of the moderately stress-tolerant generalists (Janišová et al., 2014; Filibeck et al., 2019). On the contrary, harsh microhabitats were preferred by weeds, since in these habitats, besides weeds mostly stress-tolerant specialists were present, which – due to the trade-off between stress tolerance and competitive ability – were not able to outcompete establishing weed species (Filibeck et al., 2019). In the mild north-facing slopes specialists and generalists with a good competitive ability could effectively suppress weeds. These results suggest that even though a certain level of stress can support the resistance of dry grasslands against the establishment of undesirable species, in the harshest microhabitats stress levels also suppress competitor specialists and generalists which – for example, after a disturbance event – can lead to the establishment of weeds arriving from the neighbouring anthropogenic landscape matrix (see also Yates et al., 2019).

As many mounds in the western part of the Eurasian steppe zone are embedded in transformed or cleared landscapes (Deák et al., 2016), propagule pressure from weeds arriving from the neighbouring anthropogenic habitats is one of the most considerable threat factors for mound vegetation. In our study we were able to identify hotspots of weed encroachment in both regions. In both study regions, weed encroachment can be the most problematic on the harsh microhabitats, especially on south and east slopes. Thus, in specific management and restoration projects, the weed hotspots identified need special attention. In Bulgaria, weed encroachment is a much less relevant issue on mounds than in grasslands, which further highlights the important role of mounds in biodiversity conservation.

4.2.5. Implications for conservation

A high diversity of microsites with different microclimates within the SNFs provides a unique possibility for communities to give an adaptive response to high between-year climatic variations or the projected anthropogenic climate change. As was reported from karst dolines (Bátori et al., 2020a) and inselbergs (Yates et al., 2019), topographically diverse habitat islands with diverse microclimates can mitigate local extinction under climate change by acting as microrefugia, if their microclimatic variation lies within the range of predicted climate change and they decouple the site climate from the regional climate (Keppel et al., 2012). The high temperature variations measured on the mounds studied likely exceed the temperature change predicted by the IPCC (increasing global temperatures by 2–4.5 °C by 2100; Meehl et al., 2007). Thus they can support the maintenance of climate-sensitive species, allowing them to track suitable microclimates locally by a short-distance migration, since mild and harsh microhabitats are available over very short distances (Scherrer and Körner, 2010; Keppel et al., 2012). Besides providing a possibility for an adaptive response under a changing climate, the high biodiversity maintained by the various

microhabitats of SNFs provides a potential beneficial tool for conservation. When SNFs such as mounds are involved in habitat restoration projects (e.g. by using them as core areas and restoring their buffer), they can serve as sources of a large number of target species adapted to various environmental conditions which can later spill over into the neighbouring landscape (Deák et al., 2016).

Our findings highlight that SNFs have a crucial conservation importance in plain landscapes, which cover one third of the global land area (Brown et al., 1992). We found that even landforms, which are only a few metres high, can introduce a large variation of environmental heterogeneity into these areas. Besides the more than half a million Eurasian mounds, there are also many analogous and globally widespread landforms (inselbergs – de Paula et al., 2019, dolines – Bátorai et al., 2020a, mounds built by ecosystem engineering rodents – Valkó et al., 2020) that can have a similar function in introducing EH to environmentally homogeneous landscapes, and therefore driving local and landscape-scale diversity patterns within these landscapes.

5. Conclusions

We revealed that even at the intermediate spatial scale typical of SNFs, topography is an important driver of other abiotic components of EH such as heterogeneity in the microclimate and the soil. A high EH leads to the co-existence of contrasting constantly mild and harsh microsites, and also microsites characterised by high daily microclimatic variations. A general conclusion of our study is that besides providing a high abiotic EH locally, SNFs with a complex topography can also introduce EH into otherwise environmentally homogeneous landscapes, since their abiotic environmental conditions differ from the plain areas. We revealed that heterogeneity in abiotic EH components is considerably interrelated with biotic EH components. Microsites within SNFs characterised by different abiotic environmental conditions function as contrasting microhabitats containing unique plant species compositions. As shown by our study, microhabitats on the SNFs can provide safe havens for unique specialists, which become rare or extinct in the surrounding areas. Due to the high level of EH, despite the small available area and isolated state of the studied SNFs, species typical of contrasting habitat types co-occurred even within a couple of metres. Hence, they can act as biodiversity hotspots in otherwise degraded landscapes.

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CRedit authorship contribution statement

Field data collection was done by BD, OV, AK, RK, and KL in Hungary and by BD, OV, IA, AK, RK, KL, SP, and DS in Bulgaria. Data preparation was performed by BD, OV, ZR, BK, RK and FB. Data analyses were performed by ZR and BK. The first draft of the manuscript was written by BD and OV, and all authors commented on previous versions of the manuscript. All authors contributed to the study conception and design, and read and approved the final manuscript.

Declaration of competing interest

The authors declare no conflict of interest.

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