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## Heterogeneity in microclimate and soil parameters support diverse and unique vegetation on small natural features

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Small natural features (SNFs) are small landmarks that differ in their abiotic characteristics from the surrounding landscape. SNFs, such as road verges, midfield islets, rocky outcrops and ancient burial mounds, provide safe havens for grassland specialist species in human-modified landscapes; therefore, their great ecological importance is in contrast to their small size. SNFs often have a high topographical heterogeneity and a related high variability in abiotic conditions; therefore, they provide a unique opportunity for establishing links between environmental heterogeneity (EH) and biodiversity. We investigated the EH components of topographically heterogeneous SNFs in a comprehensive framework, by linking environmental and biotic parameters. We studied ancient millennia-old burial mounds built by nomadic steppic tribes that are 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 mound 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 list and 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 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.