Received: 11 October 2022 | Revised: 10 June 2023 | Accepted: 12 June 2023

DOI: 10.1111/cobi.14148

Conservation Biology

CONTRIBUTED PAPERS

Contribution of cultural heritage values to steppe conservation on ancient burial mounds of Eurasia

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Impact statement: Cultural values related to ancient historical sites can effectively contribute to

Abstract

Civilizations, including ancient ones, have shaped global ecosystems in many ways through coevolution of landscapes and humans. However, the cultural legacies of ancient and lost civilizations are rarely considered in the conservation of the Eurasian steppe biome. We used a data set containing more than 1000 records on localities, land cover, protection status, and cultural values related to ancient steppic burial mounds (*kurgans*); we evaluated how these iconic and widespread landmarks can contribute to grassland conservation in the Eurasian steppes, which is one of the most endangered biomes on Earth. Using Bayesian steppe conservation in transformed landscapes of Eurasia.

Funding information
Narodowe Centrum Nauki, Grant/Award Number: DEC-2013/09/N/NZ8/03234; Scientific Research Committee, Poland; Hungarian Scientific Research Fund, Grant/Award Numbers: NKFI FK 135329, NKFI KKP 144096, NKFIH KDP 967901, NKFIH KKP 133839; Magyar Tudományos Akadémia, Grant/Award Number: János Bolyai Research Scholarship; Bulgarian National Science Fund, Grant/Award Numbers: contract КП, –, 06-H21/2, 2018; Polish Ministry of Science and High Education

logistic generalized regressions and proportional odds logistic regressions, we examined the potential of mounds to preserve grasslands in landscapes with different levels of land-use transformation. We also compared the conservation potential of mounds inside and outside protected areas and assessed whether local cultural values support the maintenance of grasslands on them. Kurgans were of great importance in preserving grasslands in transformed landscapes outside protected areas, where they sometimes acted as habitat islands that contributed to habitat conservation and improved habitat connectivity. In addition to steep slopes hindering ploughing, when mounds had cultural value for local communities, the probability of grassland occurrence on kurgans almost doubled. Because the estimated number of steppic mounds is about 600,000 and similar historical features exist on all continents, our results may be applicable at a global level. Our results also suggested that an integrative socioecological approach in conservation might support the positive synergistic effects of conservation, landscape, and cultural values.

KEYWORDS
grassland, land use change, sacred natural sites, agricultural landscape, biodiversity, protected areas, habitat island, landscape connectivity

Contribución de los valores culturales para la conservación esteparia en los antiguos montículos funerarios de Eurasia

Resumen: Las civilizaciones modernas y antiguas han moldeado de muchas maneras los ecosistemas globales mediante la coevolución del paisaje y la humanidad. Sin embargo, pocas veces se considera el legado cultural de las civilizaciones perdidas o antiguas para la conservación del bioma de la estepa euroasiática. Usamos un conjunto de datos que contiene más de 1,000 registros de las localidades, cobertura del suelo, estado de protección y valores culturales relacionados con los antiguos montículos funerarios de esta estepa (*kurgans*). Después analizamos cómo estos símbolos icónicos y distribuidos extensamente pueden contribuir a la conservación de los pastizales en la estepa euroasiática, uno de los biomas en mayor peligro de extinción. Analizamos el potencial de conservación de los montículos en paisajes con diferentes niveles de transformación en el uso de suelo mediante regresiones logísticas generalizadas bayesianas y regresiones logísticas de probabilidades proporcionales. También comparamos el potencial de conservación de los montículos dentro y fuera de las áreas protegidas y evaluamos si los valores culturales locales conservan los pastizales dentro de estas mismas áreas. Los *kurgans* fueron de gran importancia para la conservación de los pastizales en los paisajes transformados ubicados fuera de las áreas protegidas, en donde llegaron a fungir como hábitats aislados que contribuyeron a la conservación y conectividad del hábitat. Además de que las pendientes pronunciadas impiden el arado, cuando los montículos contaban con valor cultural para las comunidades locales, la probabilidad de que el pastizal se ubicara sobre un *kurgan* casi se duplicó. Ya que se estima que el número de montículos esteparios ronda los 6,000 y que rasgos históricos similares existen en todos los continentes, nuestros resultados pueden aplicarse a nivel global. Nuestros resultados también sugieren que una estrategia socioecológica integradora para la conservación podría respaldar los efectos sinérgicos positivos de la conservación, el paisaje y los valores culturales.

PALABRAS CLAVE
áreas protegidas, biodiversidad, cambio de uso de suelo, conectividad de paisaje, hábitat aislado, pastizal, sitios naturales sagrados

INTRODUCTION

Grasslands cover 26% of Earth's terrestrial area and play a crucial role in agricultural production and the provision of essential ecosystem services (Dixon et al., 2014; Terrer et al., 2021). The vast Eurasian steppe contains the largest proportion of global temperate grasslands (>10 million km^2) (Kirschner et al., 2020; Wesche et al., 2016). Steppe grasslands formed under continental climate, and their dry conditions harbor high biodiversity and a large number of endemic plant and animal species (Chytrý et al., 2022; Kirschner et al., 2020). The extensive grasslands of the Eurasian steppe belt provided habitat for large herds of migrating herbivores in prehistoric times and were later used as pastures for livestock; this use affected the lifestyle of local human populations. Pastoral communities and their grazing herds have been an integral part of these open landscapes for millennia, and they formed the habitat structure and species composition of vast areas (Ventresca Miller et al., 2020).

Civilizations, including ancient ones, have shaped global ecosystems in many ways through a coevolution of landscapes and humans. However, the cultural legacy of ancient and lost civilizations is rarely considered in biodiversity conservation in the steppe biome. During the Late Copper and Early Bronze Ages (3100–2500 BC), the extensive grasslands of the Pontic-Caspian steppes witnessed the rise of ancient nomadic herders, the Yamnaya culture, which profoundly shaped the history of Europe (Wilkin et al., 2021). Due to many technological advances, such as the domestication of the horse, horse traction, and bulk wagon transport, and a shift in human diet toward meat and dairy, this prehistoric pastoralist society was able to expand thousands of kilometers along the Eurasian steppes, which provided suitable environmental conditions for its nomadic herder lifestyle (Wilkin et al., 2021). The Yamnaya expansion extended over an area 6000 km wide that reached Central Europe in the West and the Altai Mountains in the East (Allentoft et al., 2015; Haak et al., 2015). By fundamentally transforming the composition of human genetic diversity in Europe and introducing the basics of the currently spoken Indo-European languages, the Yamnaya, even at a distance of 5000 years, still have a considerable effect on today's Eurasian societies (Haak et al., 2015). More importantly, the Yamnaya culture has had a lasting effect on the landscape because Yamnaya burial mounds are still the most widespread human-made prehistoric structures in the Eurasian steppe landscape (Deák et al., 2016).

Ancient burial mounds (also called *kurgans* or *barrows*) typical to the Eurasian steppes are distributed from Hungary to Mongolia. Although their original number was presumably higher by an order of magnitude (millions of kurgans were destroyed during the past centuries due to agricultural intensification and infrastructure development), there are still about 400,000 to 600,000 existing kurgans in the steppes of Eurasia (Deák et al., 2016). An overwhelming proportion of kurgans were built by the Yamnayas, but both preceding and subsequent steppe cultures built kurgans during the Iron Age and in the Migration Period (Gimbutas, 2000). Originally, kurgans had a religious function, serving as burial sites and sacred places, and were and still are) visible from large distances in the vast open steppes. Most kurgans were created by piling soil on top of a pit grave (Lisetskii et al., 2016). Their diameter ranges from a few meters up to 100 m, and they are usually 0.5–15 m high. Besides steppe kurgans, there are tens of thousands of burial mounds with a similar appearance and cultural functions in Europe (e.g., Czech Republic: Hejcman et al., 2013; Germany: Dreibrodt et al., 2009; England: Andrews & Fernandez-Jalvo, 2012; Denmark: Andersen, 2012) and the United States (Steponaitis, 1986). All kurgans can be considered an important element of cultural heritage. Even after the disappearance of the peoples who built them, in many cases they are considered sacred sites to this day, which adds to their cultural value. Subsequent peoples used kurgans as burial places, built sacral buildings and objects on them, and included kurgans in their folklore (Deák et al., 2019).

Recent ecological studies revealed that millennia-old steppic burial mounds are also important for the maintenance of steppe biodiversity in natural landscapes of central Asia characterized by vast relatively pristine grasslands (Deák et al., 2017) and in transformed European landscapes characterized by croplands and afforested and urban areas (Apostolova et al., 2022; Deák et al., 2016; Dembicz et al., 2020; Sudnik-Wójcikowska et al., 2011). The biodiversity potential of kurgans covered by grasslands is consistent with the high level of environmental heterogeneity provided by steep slopes with different aspects (Lisetskii et al., 2016; Deák et al., 2021a). Despite their small size, due to the cooccurrence of various microhabitats characterized by contrasting environmental conditions, kurgans can harbor a large variety of grassland specialist plants with different habitat requirements. Enhanced species coexistence often results in high biodiversity on kurgans, which is generally higher than ordinary grassland areas of the same size (Deák et al., 2021b).

The biodiversity potential of kurgans was demonstrated by regional surveys in Ukraine (Sudnik-Wójcikowska et al., 2011), Hungary (Deák et al., 2020), and Bulgaria (Apostolova et al., 2022) (Figure 1). Despite the small overall area of the surveyed kurgans (Ukraine 106 kurgans, 100.7 ha; Hungary 138, 33.6 ha; Bulgaria 111, 32.8 ha), they hold exceptionally high plant biodiversity (Ukraine 721 species; Hungary 469; Bulgaria 1059), representing a considerable proportion of the flora of the 3 countries (Ukraine 14%, Hungary 17%, Bulgaria 26%), and a large number of rare and protected species (Ukraine 71, Hungary 73, Bulgaria 45 species). Although studies on the biodiversity of animals in kurgans are scarce, data from Hungary suggest kurgans are also important sites for animal conservation. Among red-listed invertebrate species, 21 ant, 18 orthopteran, 76 true bug, and 20 rove beetle species were recorded in 138 surveyed kurgans (Deák et al., 2020).

The steppes in which kurgans are embedded are exposed to serious threats, as are grasslands worldwide. Their area and conservation status have declined for centuries at an alarming and constant rate (Dixon et al., 2014; Wesche et al., 2016). Protection of steppe ecosystems is especially challenging because overall coverage and mean individual size of protected areas (PAs) are lower than in any another other biome (Kirschner et al., 2020; Wesche et al., 2016). Similar to other grassland ecosystems, the most serious threat to steppes is habitat loss due to conversion to croplands or forest plantations and urbanization (Biró et al., 2018; Kamp et al., 2016). In the western part of the steppe biome, the last remnants of large and near-natural steppes have been included in the network of PAs. However, in intensively used lowland landscapes, the coverage of PAs is generally extremely low compared with mountainous regions because of the high human population density and competition for development of available fertile land (Bhagwat & Rutte, 2006).

Although in densely populated and intensively used agricultural landscapes remaining small grassland fragments might

FIGURE 1 Examples of kurgans in Ukraine, Hungary, and Bulgaria preserving grassland vegetation and typical red-listed species confined to them. Photo credits: I.I.M. (1–4); B.D. (5–9), I.A. (10–12).

be of outstanding importance, their conservation poses great challenges due to their small size and scattered distribution (Dudley et al., 2009; Maxwell et al., 2020). However, grassland islands outside PAs play a crucial role in maintaining biodiversity and grassland-related ecosystem services and provide functional spatial connections between meta-populations of grassland biota (Maxwell et al., 2020).

Studies focusing on certain regions show that millennia-old kurgans that hold dry grasslands can fulfill an important ecological role by functioning as habitat islands and providing refuge for grassland species in transformed landscapes (Apostolova et al., 2022). Deák et al. 2020; Deák et al., 2020; Dembicz et al., 2020; Sudnik-Wójcikowska et al., 2011 point out that kurgans surrounded by arable land, but that still have grassland vegetation have numbers of grassland plant and invertebrate species comparable to those in PAs characterized by seminatural landscapes. These and other studies (Dembicz et al., 2020; Sudnik-Wójcikowska et al., 2011) suggest that the probable reason for the long-term existence of island-like grassland patches on the kurgans is that the steep slopes prevent ploughing.

Although several studies focused on the conservation and ecological roles of kurgans, an important aspect has not been explored: how cultural and spiritual values bound to the kurgans support the preservation of conservation values. The importance of sites with spiritual significance to people (so-called sacred natural site [SNS]) is increasingly recognized in nature conservation globally and can be regarded as the oldest human institution to support habitat protection (Wild & McLeod, 2008). An SNS can be associated with natural (e.g., single trees, sacred grooves, rivers, or mountains) and built features (e.g., temples, shrines, or old cemeteries) found on all continents (Zannini et al., 2022; Dudley et al., 2009). Because their existence depends on the willingness of the local population and their beliefs and practices (such as traditional zanni, extensive management and bans on overuse of natural resources) associated with SNSs, these sites have a high potential for conserving natural areas even outside official nature reserves (Bhagwat & Rutte, 2006; Dudley et al., 2009). Although SNSs occur globally, scientific studies focusing on their conservation potential mostly focus on central Africa, southern Asia, and western and southern Europe (Zannini et al., 2022; Deil et al., 2005; Frascaroli et al., 2016).

Despite the high cultural and conservation importance of kurgans, there is a lack of knowledge of their numbers, locations, conservation status, and cultural value in most countries of the steppe biome. Databases containing information relevant to conservation, management, and monitoring are nonexistent in most countries. We aimed to help fill this knowledge

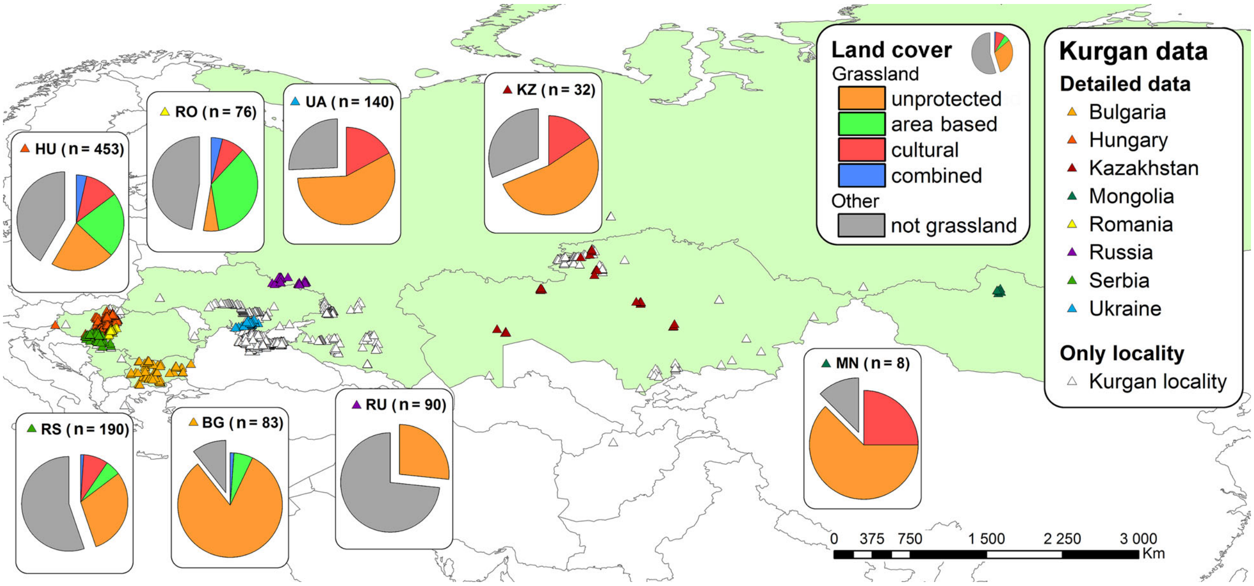

FIGURE 2 Kurgans registered in the Eurasian Kurgan Database, proportion of kurgans area covered by grasslands by protection category (Table 1), and proportion of area that is not grassland (light green, countries from which we had data; numbers in parentheses, number of kurgans from which detailed data were available by country (names abbreviated).

gap by developing an open access, up-to-date georeferenced kurgan inventory that can provide a comprehensive overview of the locations and characteristics of kurgans at a continental level (Figure 2). Some of us founded and maintain the Eurasian Kurgan Database (EKDB) (https://openbiomaps.org/projects/kurgan) (Deák, 2019; Deák et al., 2019), which contains essential information on the conservation status of kurgans over a wide geographic range, including understudied regions (Deák et al., 2019).

Although there are separate regional studies from many countries focusing on certain aspects of the conservation potential of kurgans, their role has not been sufficiently explored on a large spatial scale. By using an extensive data set covering large geographic extents, we explored the role of kurgans in conserving grassland vegetation inside and outside PAs. We also aimed to fill a knowledge gap related to the link between cultural and conservation values on kurgans. We focused especially on the highly transformed European steppe regions, where conserving the remaining grassland fragments is a crucial problem, but we also considered Asian steppes. We addressed the following questions: is there a difference between the occurrence probability of grasslands on kurgans inside and outside PAs and how does the presence of cultural values contribute to the occurrence probability of grasslands on kurgans

METHODS

Kurgan data

We used kurgan data uploaded to the EKDB (given above). The EKDB, which has an open-source database framework (OpenBioMaps; Bán et al., 2022), is a public, online database providing interfaces for uploading and accessing kurgan-related data for a wide spectrum of users. Because the EKDB was developed as a citizen science tool, the attributes in the data forms were selected considering that data providers are not exclusively biologists or geographers. Therefore, the necessary data can be reliably recognized or estimated without professional training and can be recorded using GPS and mobile phone cameras. This allows for coverage of a large geographic region and to collect a large number of records. Besides the name of the kurgan and its geographic position, detailed data on the physical attributes, landscape context, conservational status, and its cultural values can be collected in the EKDB. The database also allows photos of the surveyed kurgans to be added. Currently, the EKDB contains 3813 records (detailed data on 1072 kurgans and a further 2741 kurgan localities). We used a subset of the EKDB data that we collected. Data supporting the findings of this study are available in figshare (https://figshare.com/s/9c168f820745187d2b8c). Those who provided data for this article have diverse backgrounds, most are researchers, but there were also students, members of nongovernmental organization, and PA managers.

We evaluated only the records with detailed data (Deák et al., 2022), and kurgan locations were used only to upscale our results. The surveyed kurgans are in 8 countries that contain zonal or extrazonal steppes or forest steppes. Although we used the largest available data set on kurgans, there are still many underrepresented regions, such as Kazakhstan and Mongolia, and additional regions with steppe vegetation that are not covered by the database yet (e.g., Turkey, Iran, and China). The literature suggests the presence of a large number of kurgans in eastern steppe regions, but they are unexplored (Deák et al., 2016).

We focused on the presence of grassland on the kurgans, cover of grassland in the surrounding landscape, presence of cultural values related to kurgans, and protection status of the kurgan (Table 1). Surveyors were asked to record the presence or absence of grassland vegetation on each kurgan. Only grasslands in a good state of preservation (i.e., closed grassland structure with a dominance of native dry grassland species and a small proportion of weedy and invasive species) were considered. The number of kurgans reported in the EKDB may show a slight bias toward kurgans covered with grasslands in a good state of preservation because during data collection some surveyors might favor kurgans that were special in some way, resulting in overrepresentation of kurgans covered with grasslands.

We used the percent cover of grasslands in the surrounding landscape to estimate the level of landscape transformation around kurgans. We considered grasslands in a good state of preservation that could serve as habitat for steppe grassland species (the same criteria as for grasslands on kurgans, see above).

Surveyors visually estimated the total cover of grasslands within a 500-m radius of each kurgan on a 6-level ordinal scale (Table 1). The threshold to detect grasslands was approximately 0.1 ha (similar to the threshold applied in previous studies, such as Deák et al., [2021b]). Because we aimed to use the cover of grasslands to characterize the landscape around the kurgans on a rough (6-level) scale, we did not strive to detect tiny grassland fragments because focusing on small fragments would have enormously increased the field-survey efforts. Furthermore, we had to use this semiquantitative method instead of GIS, because there are few high-quality maps for many of the study areas.

In the case of cultural values related to the kurgans, we considered any visible signs of sacred objects, such as churches, graveyards, sacred stone pillars, and so on (complete list in Appendices S1–S2). We also considered all known nonmaterial cultural values (such as the mention of the kurgan in sagas). We did not perform a systematic search of the literature to explore the full range of nonmaterial values because they generally can be found only in local nonscientific literature. Such a search was beyond the scope of this study.

During data processing, B. D., A. B., and F. B. independently validated each kurgan data record. We used the photos uploaded by the data providers to validate the presence and quality of grasslands and the presence of cultural objects on the kurgans. The estimated cover of grasslands in the landscape were validated using the orthophotos in Google Maps (Google, 2022) and Bing Maps (Bing Maps, 2022), and the layers of pasture and natural grassland classes provided by the Corine Land Cover map (European Environment Agency 2018) in countries where they were available. For data processing, we used the QGIS program (QGIS Development Team). In the very few cases where we found any inconsistency in the reported data, we omitted the data record from the analyses.

We used the thematic layers of the World Database on Protected Areas (WDPA) (WDPA, 2022) to identify kurgans in PAs designated for nature conservation. We considered all the types of PAs listed in the WDPA, such as national PAs and EU PAs (i.e., Natura 2000 sites designated according to the Habitats Directive). The exceptions were special protection

TABLE 1 Variables used in the analyses of the probability of grassland occurrence in kurgans and in the landscape.

Variable	Variable type	Relevance	Type of collected data
Land-cover type grassland	Response variable[a,b]	Presence of grassland on kurgans one of the most important proxies for estimating conservation value of the kurgan	Binomial: grasslands present or absent
Cover of grasslands within a 500-m radius of the kurgan	Response[c] and explanatory variable[b]	Percent area of grassland cover in the landscape; a proxy for estimating level of landscape transformation and intensity of land use	Ordinal: 0, grasslands absent; 1, 1–20%; 2, 21–40%; 3, 41–60%; 4, 61–80%; 5, 81–100%
Country	Explanatory variable[a,c]	Proxy for geographical position of the kurgan	Categorical (6 countries in the models)
Protection status	Explanatory variable[a,c]	Information on potential source of protection; important for comparing effectiveness of legal protection and protection provided voluntarily by local population	Categorical: unprotected; area-based protection[d]; cultural protection; combined area based and cultural

[a]Variable used to explore the effect of protection status and country on grassland presence.
[b]Variable used to determine the effect of grassland cover in the landscape on grassland presence on kurgans.
[c]Variable used to explore the effect of protection status and country on grassland cover in the landscape.
[d]Located inside protected areas.

areas because these are primarily designated for bird conservation and do not necessarily focus on preserving natural or seminatural habitats. We also did not consider any protection regulations related to the archaeological values of the mounds because these regulations generally focus only on the structure of the kurgan and generally do not prohibit destructive land-use practices (e.g., ploughing or afforestation) that negatively affect the natural of the mound (Deák et al., 2016).

Based on their protection status and presence or absence of cultural values on the kurgans, we categorized the kurgans into 4 groups: unprotected, outside PAs and of no cultural value; area-based protection, inside PAs and of no cultural value; cultural protection, outside PAs and of cultural value; combined protection, inside PAs and of cultural value (Table 1).

Statistical analyses

All data handling and statistical analyses were performed in R (R Core Team, 2022). The analytical workflow is summarized in Appendix S3. To explore how kurgan protection status (unprotected, area-based protection, cultural protection, combined protection), grassland cover within a 500-m radius buffer around the kurgan, and the country where the kurgan is located (explanatory variables) affect the presence or absence of grassland on the kurgan (binomial response variable [Table 1]), we used Bayesian logistic generalized regression models with the R package arm (Gelman & Su, 2020). Using this modeling approach, we could explicitly quantify the occurrence probability of grasslands on kurgans as a function of protection status, grassland cover around kurgans, and the country of origin of the kurgans. For these logistic generalized regression models, we used Bayesian generalized linear models because they enable the estimation of reasonable standard errors even for low-variability or invariant group levels (e.g., in the case of complete separation). We used the quasi-binomial model family in logistic regression models to control for the imbalanced data distribution caused by differences in the amount of kurgan data from different countries.

To explore the differences in grassland cover in the surrounding landscape (ordinal response variable) between the kurgan protection categories and countries (explanatory variables), we used proportional odds logistic regression models with the R package MASS. Such models are ideal to investigate effects shaping discrete and ordered scores. Therefore, we were able to quantify expected score estimates at specific explanatory variable values. Given the low number of kurgan data reported from Kazakhstan (32) and Mongolia (8), we excluded these countries from the statistical analyses, but considered them in the "Discussion."

Due to the imbalanced data distribution among countries, we specified weights based on the proportion of observations originating from different countries in all models. Specifically, we used inverse probability weighting ($w_i = 1 - p_{Ci}$, where w_i is the weight for the ith observation and p_{Ci} is the proportion of observations originating in the country [C] to which the ith observation belongs) to control for disparate sample sizes from different countries. To avoid multicollinearity (correlations between explanatory variables) and biases from imbalanced cooccurrences of levels of multiple binomial, ordinal, and categorical explanatory variables (for binomial logistic models the presence of grassland on kurgans: grassland cover in the neighboring landscape, kurgan protection category, and country; for proportional odds logistic models of grassland cover in the surrounding landscape: kurgan protection category and country), we fitted separate models for each pair of responses and explanatory variables. Estimated marginal means (EMMs) and contrasts from ordinal models, mean probabilities, and odds ratios from logistic models were acquired using the emmeans R-package (Lenth, 2019). We adjusted the p values of the fitted models with Bonferroni's method to decrease the probability of type I errors. In "Results," we report EMMs and contrasts for ordinal models and estimated mean probabilities and odds ratios for binomial models.

RESULTS

Fifth-eight percent of kurgans were covered by grasslands. Kurgans in Russia had the lowest probability of grassland cover (27.0%), whereas Bulgarian (89.8%) and Ukrainian (74.5%) kurgans had the highest probability. In Hungary (59.3%), Romania (51.8%), and Serbia (44.9%), the probability of grassland cover on kurgans was intermediate (Figure 3 & Appendices S4−S6). The landscape surrounding the kurgans was highly transformed in Russia and Ukraine, resulting in low cover of grassland. Grassland cover in the landscape was the highest in Romania and Bulgaria and intermediate in Hungary and Serbia (Figure 4 & Appendices S7−S9).

In landscapes where grasslands were absent, the probability of grassland presence on kurgans was the lowest (39%) (Figure 5 & Appendices S10–S12). In landscapes where the grassland cover in the neighboring landscape ranged from 1% to 40%, the probability of grassland presence on the kurgans was almost 3 times higher (odds ratio 0.31) and reached up to 71%. In landscapes with grassland cover >40%, the probability for grassland presence on kurgans increased considerably and was the highest (>95%).

Kurgans with area-based (77.5%), cultural (66.5%), and combined (73.0%) protection held grasslands with a significantly higher probability than unprotected kurgans (50.8%) (Figure 3 & Appendices S13–S15). The cover of grasslands in the surrounding landscape was the highest in the case of kurgans with area-based or combined protection. In the case of unprotected kurgans and kurgans with cultural protection, the grassland cover in the landscapes was equally low (Figure 4 & Appendices S16–S18).

DISCUSSION

Conservation function and level of landscape transformation

Even in heavily transformed landscapes, where grasslands were almost completely missing, kurgans had a great potential to

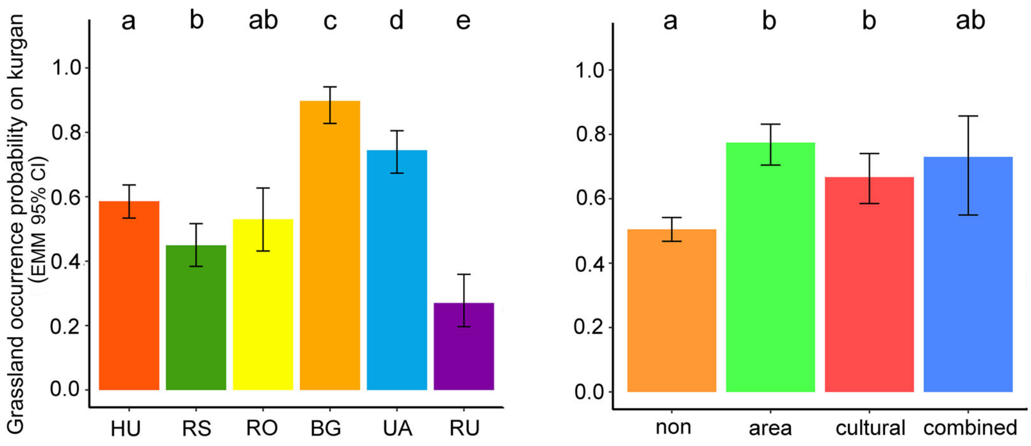

FIGURE 3 Estimated marginal mean (EMM) probability (95% confidence interval) of grassland occurrence on 1032 kurgans in Hungary (HU), Serbia (RS), Romania (RO), Bulgaria (BG), Ukraine (UA), and Russia (RU) (left) and on kurgans with different protection types (non, unprotected; area, protected area; cultural, cultural protection; combined, area and cultural protection; differing letters, significant differences between groups [contrasts from Bayesian logistic generalized regression models, $p \leq 0.05$]).

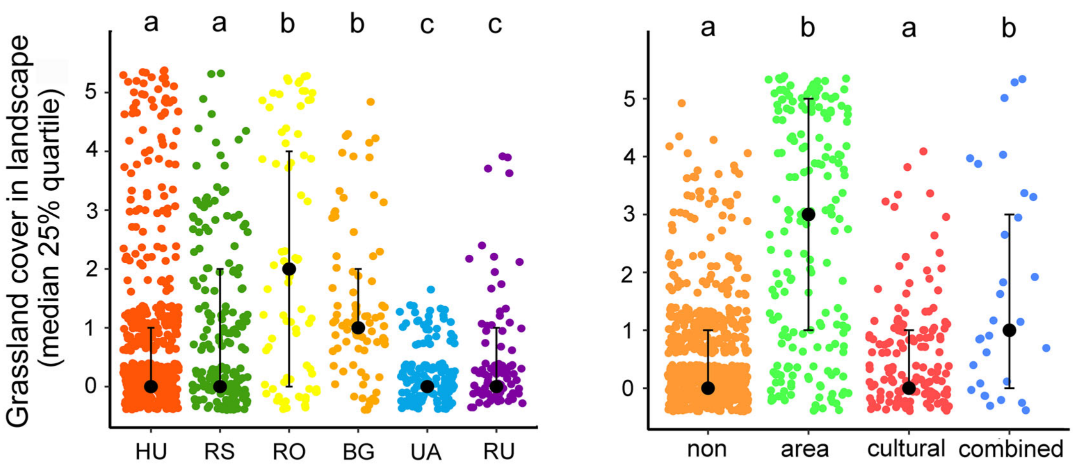

FIGURE 4 Grassland cover in the landscape within a 500-m radius of 1032 kurgans in Hungary (HU), Serbia (RS), Romania (RO), Bulgaria (BG), Ukraine (UA), and Russia (left) and with different protection types (non, unprotected; area, protected area; cultural, cultural protection; combined, area and cultural protection) (right) (grassland cover: 0, grasslands absent; 1, 1−20% grassland cover; 2, 21−40%; 3, 41−60%; 4, 61−80%; 5, 81−100%; black dots, median; black lines, 25% quartile range; differing letters, significant differences between groups [contrasts from proportional odds logistic regression model, $p \leq 0.05$]).

preserve grasslands. This suggests that in such landscapes, kurgans with grasslands could function as habitat islands, and, in this sense, their function is similar to that of other small natural features, such as road verges, ravines, forest fringes, hedgerows, midfield islets, and old trees, which occur in- and outside steppe and forest steppe biomes (Hunter et al., 2017). This conservation role might be especially important in countries where, due to large-scale land transformation, grassland cover in landscape is very small. These countries were Ukraine and Russia, where transformation of steppe grasslands to croplands began in the 18th century and accelerated in 1920s with the development of agricultural machinery (Smelansky, Tishkov, 2012). In the entire former Soviet Union, approximately 452,000 km^2 of grasslands were converted to cropland from 1954 to 1963 during the Virgin Land Campaign (Smelansky, Tishkov, 2012; Kamp et al., 2016). Despite the increasing human population densities and the large expansion of the croplands in the past centuries, somewhat larger amount of grassland cover were preserved in Hungarian and Serbian study sites, likely due to a traditional land-use system based on the presence of numerous small farms, each sustaining a certain area of grasslands for forage (Biró et al., 2018; Deák et al., 2021b).

Our results suggest that in landscapes where the cover of grasslands ranges from 1% to 40%, kurgans that have well-preserved grasslands can be integral elements of the landscape-level grassland network and green infrastructure. By acting as stepping stones, kurgans can enhance the functional spatial connectivity between the remaining grassland fragments

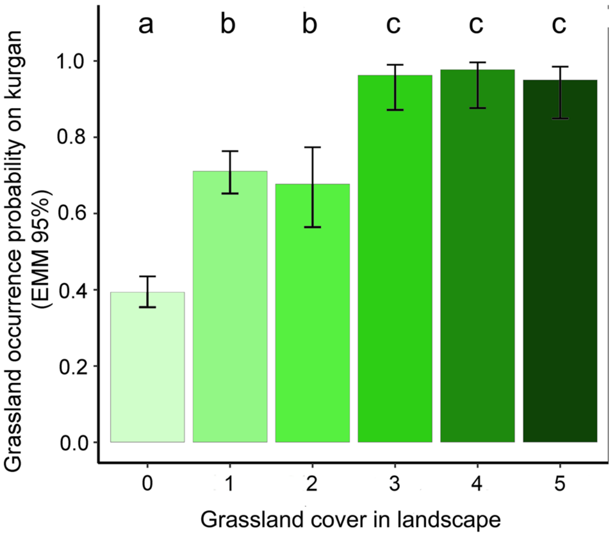

FIGURE 5 Estimated marginal mean (EMM) (95% confidence interval) of the occurrence of grasslands on 1032 kurgans as a function of grassland cover within a 500-m radius (grassland cover: 0, grasslands absent; 1, 1−20% grassland cover; 2, 21−40%; 3, 41−60%; 4, 61−80%; 5, 81−100%; differing letters, significant differences between groups [contrasts from Bayesian logistic generalized regression models, $p \leq 0.05$]).

and contribute to the maintenance of meta-population connections of grassland species, especially for taxa with good dispersal abilities (Deák et al., 2020).

Landscapes with a grassland share of over 40% are typical for PAs of many European regions (e.g., Bulgaria or Romania) and for some Asian countries (e.g., Mongolia and Kazakhstan), where most of the remaining near-natural temperate grasslands in the world occur (Kamp et al., 2016). In Kazakhstan and Mongolia, all the kurgans surveyed were covered with grasslands, except those that were built from stones. In these landscapes, the conservation importance of kurgans is linked to their high biodiversity and unique flora (Deák et al., 2017). Studies from Europe (Lisetskii et al., 2016; Deák et al., 2021a) and Central Asia (Deák et al., 2017) show that due to their specific environmental conditions, kurgans often harbor a large number of grassland species that are underrepresented in neighboring plain landscapes. Typical examples are the appearance of forest steppe plants on the north-facing slopes (characterized by cool and moist microclimate) of kurgans in the steppe biome (Deák et al., 2017) and steppe plants under the extreme environmental conditions on the top and on the south-facing slopes of kurgans in the forest steppe biome (Deák et al., 2021a). In this sense, the function of the kurgans is analogous to that of landmarks, such as inselbergs and dolines, which are also characterized by a high level of topographical heterogeneity (Ottaviani et al., 2016; Bátori et al., 2021).

Kurgans and PAs in grassland conservation

Our results confirmed that kurgans inside PAs could indirectly benefit from area-based protection (e.g., from the presence of extensive management measures and prohibition of land transformation) even if originally the PA was not focused on the kurgan itself because of its small size relative to the size of the PAs. This is a promising but evident pattern because PAs were designated and managed for preserving landscapes that primarily held a high proportion of natural or seminatural areas. In such landscapes, kurgans were less affected by anthropogenic disturbances even before they became part of the PA.

Kurgans outside PAs greatly outnumbered those inside and had a high potential to preserve grasslands. The fact that even outside PAs a large proportion of kurgans contained grasslands is especially important from a conservation perspective. Previous studies show that kurgans outside PAs could hold a similar number of grassland specialist taxa as kurgans inside PAs or even plain grasslands with a comparable size (Moysiyenko et al., 2014; Deák et al., 2020). In countries in the western part of the steppe biome (such as Hungary and Serbia), unprotected kurgans were typically embedded in agricultural landscapes with little grassland cover. In Hungary, kurgans are considered a protected landscape element and covered under regulations connected to the Nature Conservation Law. Kurgans have recently been included in the Single Area Payment Scheme (SAPS) of the European Union's Common Agricultural Policy. Our results suggest this combined protection scheme resulted in a slightly higher probability of grassland occurrence on kurgans in Hungary compared with neighboring Central European countries, where kurgans are not considered in the SAPS system. The primary aim of SAPS-related regulations is to suppress farming on kurgans to prevent soil erosion and provide good environmental conditions for spontaneous succession; they do not directly support grassland recovery.

Ploughing on kurgans with steep slopes can be difficult with modern agricultural machinery and was even more challenging in the ages of large landscape transformation with less effective agricultural tools (Deák et al., 2016). The protective effect of steep slopes is especially apparent in Bulgaria, where mounds generally have extremely steep slopes that make them highly unsuitable and unattractive for farming in the vast plain landscapes, where large areas could be agriculturally developed (Apostolova et al., 2022). In this sense, kurgans are similar to landscape features, such as rocky outcrops and ravines, that escape the plough due to their physical attributes (Dembicz et al., 2020; Hunter et al., 2017).

Relevance of cultural values in conservation

A considerable proportion of kurgans had various elements of cultural value, such as historical buildings, statues, memorial places, medieval roads, border marks, and nonmaterial values (altogether 57 types of cultural values; Appendices S1 & S2). However, because kurgans were built millennia ago, most of the ancient sacred objects are no longer present. But as our data showed, ancient stone pillars and statues are still visible on kurgans in some sparsely populated remote areas in Kazakhstan and Mongolia. Although the ancient faith of the builders has mostly disappeared, subsequent cultures realized the sacredness related to the kurgans, which resulted in the continuation of their sacred function (Deák et al., 2019). As our data showed, the original burial function of kurgans exists today. Accordingly, many kurgans have cemeteries with graves dating back to medieval times. In Hungary and Serbia, as indicated by numerous sacral buildings and objects, Christians used kurgans as sacred focal points since historical times. In these countries kurgans have often been used as foundations for crosses, calvaries, chapels, and even churches since the 10th century, when Christianity became the state religion.

Cultural protection almost doubled the chance of grassland presence on kurgans outside PAs compared with those that had no cultural value. This pattern is especially important because culturally protected kurgans are generally found in densely populated, heavily transformed anthropogenic lowland landscapes, where grasslands are critically endangered. In this respect, kurgans have similarities with SNSs, such as churchyards, shrines, or old cemeteries, which can also preserve fragments of former natural land cover in landscapes under high anthropogenic pressure (Bhagwat & Rutte, 2006; Deil et al., 2005; Dudley et al., 2009; Frascaroli et al., 2016; Kowarik et al., 2016; Zannini et al., 2021).

Land transformation activities, such as ploughing and afforestation, were less typical on kurgans with cultural protection due to their diverse social functions and the respect of the local populations. To maintain the social functions and the well-kept appearance of such kurgans, extensive, continuous management is often provided by mowing and eliminating woody vegetation, which can also benefit grassland maintenance (Deák et al., 2020b). This phenomenon shows considerable similarities with the management of SNSs (sacred grooves, saint mountains, shrines, graveyards, or church gardens), which can be found across the globe and are traditionally extensively managed by local populations for nonproduction purposes (Zannini et al., 2021).

Conservation outlook

Our large-scale synthesis revealed that ancient burial mounds, which are the most widespread human-made landmarks in the Eurasian steppes, play a considerable role in grassland conservation. Results of previous studies show that kurgans can function as safe havens, stepping stones, or biodiversity hotspots, depending on the landscape context (Sudnik-Wójcikowska et al., 2011; Deák et al., 2020; Dembicz et al., 2020; Apostolova et al., 2020). We could upscale our findings to a larger geographic extent because grassland-covered kurgans occurred in transformed and natural landscapes in many regions of Eurasia. This suggests that kurgans can provide various ecological functions mediated by their landscape context.

By preserving the last remnants of steppe grasslands, kurgans in agricultural or peri-urban areas can serve as important elements of the landscape-level network of remaining dry grasslands and thus can efficiently support grassland conservation. This is especially important because in fertile lowland landscapes, PAs are generally small, rarely overlap with the distribution areas of many rare or protected species, and do not provide a functional connection between their metapopulations (Baranazelli et al., 2022). Taking into account the climate changes expected in the next few decades, one can conclude that a landscape-level network of seminatural habitats will be of increasingly high conservation importance in the near future (Kirschner et al., 2020). Such a green infrastructure network can allow for adaptive spatial movement of climate-sensitive species and thus contribute to maintaining their populations. Additionally, kurgans characterized by a variety of climatically contrasting microhabitats can also buffer the effect of changing climate at the site level because climate-sensitive species can easily relocate to microsites matching their environmental needs (Deák et al., 2021a).

Although highly isolated kurgans covered by grasslands have a high conservation potential, they could be negatively affected by insufficient functional connections with other grassland fragments in the landscape. Given that many steppe plants have a short-distance dispersal strategy and dispersed by mammals confined to the formerly existing natural or seminatural open landscapes, they may lose metapopulation connections on isolated kurgans. These habitat islands can become an ecological trap for plants with limited dispersal ability and lead to genetic homogenization and population decline (Habel & Schmitt, 2018). The same applies to less mobile invertebrate species, such as ants (Deák et al., 2020). Thus, in highly transformed landscapes, targeted grassland restoration measures would be needed to improve the connections among meta-populations on kurgans and other landscape elements (e.g., road verges, river banks, and rocky outcrops) that hold remnant grassland areas (Aavik & Helm, 2018).

Besides those with area-based or cultural protection, many kurgans do not have any form of protection. In the western part of the steppes, most kurgans are in croplands (Deák et al., 2016; Dembicz et al., 2020; Apostolova et al., 2022); thus, inclusion of kurgan protection in the system of agrienvironmental subsidies may offer a feasible solution for the maintenance or restoration of grasslands on the mounds. The current SAPS-based kurgan protection framework applied in Hungary is an example of this. However, these regulations predominantly focus on the prohibition of intensive land use on the kurgans and do not include active and targeted measures to support grassland restoration on formerly ploughed or degraded kurgans, which would be necessary to restore their ecosystem functions and grassland biodiversity. Considering related costs in subsidies provided based on the Common Agricultural Policy (e.g., in the form of additional support for voluntarily performed active grassland restoration) would be a nature-based solution for the restoration of kurgan-related ecosystem services, such as pollination, weed suppression, pest control, and increased landscape value. It would be advantageous to set up a general SAPS-based framework for kurgan protection in those member states of the European Union that have a large number of steppic burial mounds (e.g., Bulgaria, Poland, and Romania).

The EU Biodiversity Strategy intends to increase the area of uncultivated high-diversity landscape features (HDLFs) (e.g., hedgerows, flower strips, and riparian corridors) to at least 10%

of the utilized agricultural area by 2030. Grasslands on kurgans could also be recognized as HDLFs, forming an additional pillar for their conservation and restoration. In addition to the SAPS-based framework, kurgan protection could also be achieved with bottom-up public participation because mounds are highly recognized by local population and can thus be obvious targets of nongovernmental organizations focused on the preservation of local cultural and natural heritage (Valkó et al., 2018).

The participation of local citizens can also be a suitable tool for exploring the distribution and conservation status of the kurgans. Due to recent survey campaigns (Sudnik-Wójcikowska et al., 2011; Deák et al., 2020; Apostolova et al., 2022), we have detailed information on the location and the conservation status of kurgans in particular regions in countries mostly located in the western part of the Eurasian steppe biome. However, data are lacking for many parts of Eastern Europe and almost all parts of Asian steppes, where hundreds of thousands of kurgans are located. Also, by means of a well-designed citizen science framework, it would be possible to collect detailed data on the surrounding landscape (e.g., quality of the neighboring grassland patches) and on nonmaterial cultural values (i.e., folkloristic data). The latter might be of crucial importance because as in our case, collecting important folkloristic data is challenging, which for example, might lead to the underestimation of the positive effect of cultural protection.

A growing number of studies show that the global system of PAs does not provide a sufficient level of biodiversity protection (Wauchope et al., 2022). The effectiveness of the global PA system can be increased to some extent by designating new PAs based on improved spatial planning tools or by increasing the efficiency of protection in PAs. However, these measures all have limits because the land for PAs is also in demand for agriculture, industry, and infrastructure development. Our results highlight that to complement and support the system of PAs, it is crucial to acknowledge the conservation potential of sites that, thanks to their associated cultural values, can harbor natural land cover even in unprotected landscapes. Our results suggest that an integrative socioecological approach to conservation could support the positive synergistic effects of conservation, landscape, and cultural values.

ACKNOWLEDGMENTS

We thank G. Batdelger, M. Biró, Z. Gavrilović, D. Grabovác, R. Mirić, Z. Molnár, Z. Nagygyörgy, S. Spremo, P.I. Tóth, R. Vesović, and the entire EKDB community for their help in surveying kurgans. This study was supported by the Hungarian National Research, Development and Innovation Office (NKFI FK 135329). The work of O. V. and B. D. was supported by the Hungarian National Research, Development and Innovation Office (NKFI KKP 144096). P. B., R. G., and B. D. were supported by the Hungarian National Research, Development and Innovation Office (NKFIH KKP 133839). I. A. and G. N. were supported by the Bulgarian National Science Fund (contract КП–06-H21/2, 2018). R. G. was supported by the János Bolyai Research Scholarship of the Hungarian Academy of Sciences. I.D. was supported by the Polish National Science Centre (grant DEC-2013/09/N/NZ8/03234) and the Polish Ministry of Science and High Education. B. S. and I. M. were supported by the Scientific Research Committee, Poland (grants 2PO4G04627 and NN304081835). S. B. was supported by the NKFIH KDP 967901 grant. We are grateful to A. Huckauf for linguistic help.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Deák, B., Bede, Á., Rádai, Z., Dembicz, I., Apostolova, I., Batáry, P., Gallé, R., Tóth, C. A., Dózsai, J., Moysiyenko, I. I., Sudnik-Wójcikowska, B., Zachwatowicz, M., Nekhrizov, G., Lisetskii, F. N., Buryak, Z. A., Kis, S., Borza, S., Godó, L., Bragina, T. M., … Valkó, O. (2023). Contribution of cultural heritage values to steppe conservation on ancient burial mounds of Eurasia. *Conservation Biology*, *37,* e14148. https://doi.org/10.1111/cobi.14148