


Diversity patterns in sandy forest-steppes: a comparative study from the western and central Palearctic

Zoltán Bátori¹  · László Erdős² · András Kelemen^{3,4} · Balázs Deák⁵ · Orsolya Valkó⁵ · Róbert Gallé¹ · Tatyana M. Bragina^{6,7} · Péter János Kiss¹ · György Kröel-Dulay² · Csaba Tölgyesi¹

Received: 5 May 2017 / Revised: 20 November 2017 / Accepted: 25 November 2017 /

Published online: 30 November 2017

© Springer Science+Business Media B.V., part of Springer Nature 2017

Abstract The Palearctic forest-steppe biome is a narrow vegetation zone between the temperate forest and steppe biomes, which provides important habitats for many endangered species and represents an important hotspot of biodiversity. Although the number of studies on forest–grassland mosaics is increasing, information currently available about the general compositional and structural patterns of Eurasian forest-steppes is scarce. Our study aimed to compare the habitat structure, species composition and diversity patterns of two distant sandy forest-steppes of Eurasia. We compared 72 relevés made in the main habitat components (forest, forest edge and grassland) of sandy forest-steppes in three Hungarian and three Kazakh sites. The size of the plots was 25 m². Species number, Shannon diversity and species evenness values were calculated for each plot. Fidelity calculations and linear mixed effects models were used for the analyses. We found that the vegetation and diversity patterns of the two forest-steppes are similar and their components play important roles in maintaining landscape-scale diversity. Despite the higher species

Communicated by Daniel Sanchez Mata.

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s10531-017-1477-7>) contains supplementary material, which is available to authorized users.

✉ Zoltán Bátori
zbatory@gmail.com

¹ Department of Ecology, University of Szeged, Közép fasor 52, Szeged 6726, Hungary

² Institute of Ecology and Botany, MTA Centre for Ecological Research, Alkotmány út 2–4, Vácrátót 2163, Hungary

³ Department of Ecology, University of Debrecen, Egyetem tér 1, Debrecen 4032, Hungary

⁴ MTA's Post Doctoral Research Program, MTA TKI, Nádor utca 7, Budapest 1051, Hungary

⁵ MTA-DE Biodiversity and Ecosystem Services Research Group, Egyetem tér 1, Debrecen 4032, Hungary

⁶ Kostanay State Pedagogical Institute, Tauelsizdik Street 118, Kostanay, Kazakhstan

⁷ FSBSI AzNIIRKH, Beregovaya Street, 21 V, Rostov-on-Don, Russia

richness in Hungary, Shannon diversity was higher in Kazakhstan. The deciduous forest edges of both areas had significantly higher species richness than the neighbouring habitats (forests and grasslands); therefore they can be considered local biodiversity hotspots. Due to the special characteristics of this vegetation complex, we emphasize the high conservation value of all landscape components as a coherent system throughout the entire range of the Eurasian forest-steppe biome.

Keywords Conservation · Endemic plant · Forest edges · Hungary · Kazakhstan · World heritage site

Introduction

The Palaearctic forest-steppe is a distinct vegetation zone between the temperate forest and steppe biomes, ranging from East-Central Europe in the west almost to the Pacific Ocean in the east (Lavrenko 1969; Walter and Breckle 2002; Zlotin 2002). The main characteristic of this zone is the alternation of forest patches with grasslands, resulting in a compositionally, microclimatically and structurally complex habitat mosaic (Erdős et al. 2014). Due to the complex biotic interactions among the main components (forest, forest edge and grassland), forest-steppes play an important role in preserving many species with different habitat requirements and hence maintaining landscape-scale diversity (Molnár et al. 2012; Erdős et al. 2013a). They also provide refuges for many rare and threatened animals and plants and have been recognised as an important hotspot of biodiversity (Zlotin 2002; Habel et al. 2013; Kamp et al. 2016). In addition, forest-steppes can attain relatively high net primary production rates, considerable biomass and carbon sequestration capacity (Müller 1981; Zlotin 2002; Schultz 2005). Structurally similar grassland–forest mosaics exist in the Middle East, Central Asia, southwestern Inner Asia and in the Eastern Tibetan Plateau (cf. Wesche et al. 2016).

The canopy of the forest component in the forest-steppe biome is primarily composed of deciduous trees (*Acer*, *Betula*, *Carpinus*, *Fraxinus*, *Populus*, *Quercus*, *Tilia* and *Ulmus* spp.) in Southeast and East Europe (Horvat et al. 1974; Chibilyov 2002; Chytrý 2012; Korotchenko and Peregrym 2012; Molnár et al. 2012), deciduous (*Betula*, *Larix*, *Populus* and *Ulmus* spp.) and evergreen (*Pinus sylvestris*) trees in West Siberia, North Kazakhstan and Inner Asia (Lavrenko and Karamysheva 1993; Shahgedanova et al. 2002; Dulamsuren et al. 2005; Rachkovskaya and Bragina 2012; Mathar et al. 2016), and deciduous trees (e.g. *Betula*, *Quercus* and *Tilia* spp.) in the Far East (Ivanov 2002; Zhang et al. 2006; Liu et al. 2015). The steppe component is dominated by grasses, mainly feather grasses (*Stipa* spp.) and fescues (*Festuca* spp.) throughout the biome (Lavrenko and Karamysheva 1993; Wesche et al. 2016). The term zonal forest-steppe is used to distinguish forest-steppes whose distribution and species composition are predominantly determined by macroclimate (i.e. precipitation and temperature) from forest-steppes constrained by edaphic (i.e. soil-related) conditions (Molnár et al. 2012). For instance, the loess steppe–oak forest mosaics on chernozem soils in East-Central Europe belong to the zonal group (Borhidi et al. 2012). However, the xeric sandy grassland–forest mosaics of the biome belong to the edaphic group, since their soil is coarse textured, humus-poor and has a low water-holding capacity (Rachkovskaya and Bragina 2012; Erdős et al. 2013a). There is a discussion about forest-steppes that owe their existence to human activities (e.g. forest clearing, grazing or burning), but they cannot be considered zonal either (cf. Dulamsuren et al. 2005; Erdős et al. 2013b).

Diversity patterns of forest-steppes are determined by habitat structure and vegetation history. Species diversity of forest-steppes may be exceedingly high in areas where environmental conditions and/or anthropogenic effects have favoured both forest and grassland persistence throughout the Holocene (cf. Dengler et al. 2012; Feurdean et al. 2015; Novenko et al. 2016). Due to the relatively low canopy closure, the forest component may share a large number of plants with grasslands (Ermakov and Maltseva 1999). Therefore, the spatial mass effect (Shmida and Ellner 1984) plays a crucial role in determining species diversity and vegetation dynamics in forest-steppe ecosystems (Mathar et al. 2016). In addition, the edges of forest patches may have an important role in maintaining species diversity (Erdős et al. 2013a). Edges are essential components of ecosystems, since they control the ecological flows between habitat patches (Wiens et al. 1985; Cadenasso et al. 2003), influence landscape dynamics (Risser 1995; Peters et al. 2006) and species interactions (Fagan et al. 1999), and may serve as habitats for a wide variety of organisms (Kolasa and Zalewski 1995; Erdős et al. 2014). Edges often act as local biodiversity hotspots, because they may contain species from neighbouring communities as well as own species (Odum 1971; Pianka 1983; Risser 1995). In other cases, diversity at edges may also be intermediate (van der Maarel 1990), or similar to one of the two neighbouring communities (Erdős et al. 2011).

In Europe, extensive near-natural forest-steppes have only been preserved in areas that are less suitable for agriculture or where the level of legal protection is high (Biró et al. 2013; Zólyomi and Fekete 1994; Eliáš et al. 2013). The majority of forest-steppes has been destroyed or severely degraded by land transformation in the past centuries (Korotchenko and Peregrym 2012; Smelansky and Tishkov 2012; Deák et al. 2016). A large proportion of the steppe component has been converted into croplands and plantations of non-native trees (e.g. *Pinus nigra* and *Robinia pseudoacacia*), while many forest patches have been logged or replaced with plantations (Berg 1958; Parnikoza and Vasiluk 2011; Molnár et al. 2012). However, human impacts have been less intense in the Asian forest-steppes (Lavrenko and Karamysheva 1993; Zlotin 2002); thus, they could persist in relatively large areas. Nevertheless, the biodiversity of both European and Asian forest-steppes is experiencing novel threats posed by climate change. Climate change scenarios predict the increase of mean annual temperature and summer drought in the zone, contributing to the increase of wildfires (Kamp et al. 2016). Wildfires and uncontrolled burning may have serious negative impacts on diversity (cf. Valkó et al. 2014). These processes might lead to the decrease in the cover of forest component and increase in the cover of grassland component in the future. Unfortunately, the current system of protected areas is not entirely sufficient to maintain the biodiversity and ecosystem processes of the forest-steppe biome (e.g. Rachkovskaya and Bragina 2012; Wesche et al. 2016).

The sandy forest-steppes of Eurasia show an island-like distribution pattern within the forest-steppe biome (and sometimes in the neighbouring biomes). Their surface is characterised by slightly undulating sand dunes with humus-poor arenosols. Sandy forest-steppes have a unique flora with many species adapted to extremely dry conditions (cf. Komarov 1968–2002; Borhidi et al. 2012; Erdős et al. 2013a). The relatively high number of endemic plant taxa is related to the temporal and spatial isolation of habitats, special soil types and geomorphological diversity (Vicherek 1972; Dubyna et al. 1995; Molnár 2003). Some of these taxa (e.g. *Agropyron dasyanthum*, *Dianthus diutinus* and *D. serotinus*) are listed on the IUCN global Red List (Bilz 2011; Király and Stevanović 2011; Smekalova et al. 2011).

Sandy forest-steppes have been relatively well studied in Europe (especially in Hungary); however, information about the species composition and habitat structure of the

Asian sandy forest-steppes is scarce. Although there are evidences that forest-steppes play an important role in the preservation of many rare and threatened species, there is a lack of studies comparing the general community patterns of distant forest-steppe areas. We aimed to describe the habitat structure and diversity patterns of a Kazakh sandy forest-steppe and compare these to the westernmost sandy forest-steppe of the Palaearctic, located in Hungary. We addressed the following questions: (1) Do the plant compositional and diversity patterns of the European and Asian sandy forest-steppes resemble each other? (2) Do the components of sandy forest-steppes have a similar role in preserving plant species in both areas?

Methods

Study areas

Fieldwork was done during the summer of 2016 in two Eurasian calcareous sandy forest-steppes: the Kiskunság Sand Ridge in Central Hungary (East-Central Europe) and the Naurzum Nature Reserve in North Kazakhstan (Central Asia), located 3000 km apart from each other (Fig. 1). In both areas, the soil of the grasslands is a humus-poor sandy soil with very low water-holding capacity, whereas the soil under forest patches has slightly higher humus contents and a less extreme microclimate (Erdős et al. 2014). The surface of both areas is characterised by slightly undulating, stabilized sand dunes.

Sand dunes in Kiskunság occupy large areas on the plain between the Danube and Tisza rivers. The re-deposited alluvial sand has originated from the Danube River. The climate is continental with a strong sub-Mediterranean influence. Mean annual temperature was 11.1 °C (mean January and July temperatures were 1.1 and 22.3 °C, respectively) and mean annual rainfall was about 600 mm (mean summer rainfall was 195 mm) over the period 2005–2015 (weather data source: MTA Centre for Ecological Research; for the village of Fülöpháza). According to Magyari et al. (2010), the grasslands of the area were continuously present throughout the Holocene. Although the potential vegetation of this area is forest-steppe, it was almost completely treeless between the fifteenth and nineteenth centuries due to deforestation (Erdős et al. 2015). Agriculture and forestry led to the rapid fragmentation of sandy vegetation, thus only a few stands of sandy forest-steppes could persist for the twenty-first century (Molnár 2003). Abundant species of the xeric grasslands within our sites are *Alkanna tinctoria*, *Bothriochloa ischaemum*, *Crepis foetida* subsp. *rheodifolia*, *Dianthus serotinus*, *Euphorbia seguieriana*, *Fumana procumbens*, *Festuca vaginata*, *Koeleria glauca*, *Secale sylvestre*, *Stipa capillata* and *Stipa pennata* s.l., with a total vegetation cover of 20–75%. Forest patches have a tree canopy cover of 50–80% and are dominated by 15–20 m tall *Populus alba* trees. In the shrub layer, *Berberis vulgaris*, *Crataegus monogyna*, *Juniperus communis*, *Ligustrum vulgare* and *Rhamnus cathartica* are the most common, with a cover of 2–65%. The most abundant species of the herb layer in the forests are *Asparagus officinalis*, *Brachypodium sylvaticum*, *Calamagrostis epigejos*, *Carex flacca*, *Carex liparicarpos*, *Euphorbia cyparissias* and *Poa angustifolia*. These grasslands and forest patches are priority habitats of the Natura 2000 ecological network.

UNESCO designated the area ‘Saryarka—Steppe and Lakes of Northern Kazakhstan’ as a World Heritage Site in 2008, which includes undisturbed areas of Central Asian steppes and lakes of the Naurzum and Korgalzhyn Nature Reserves. Sandy forest-steppe is one of the most typical habitats in Naurzum. Sand has an aeolian origin. The climate is strongly

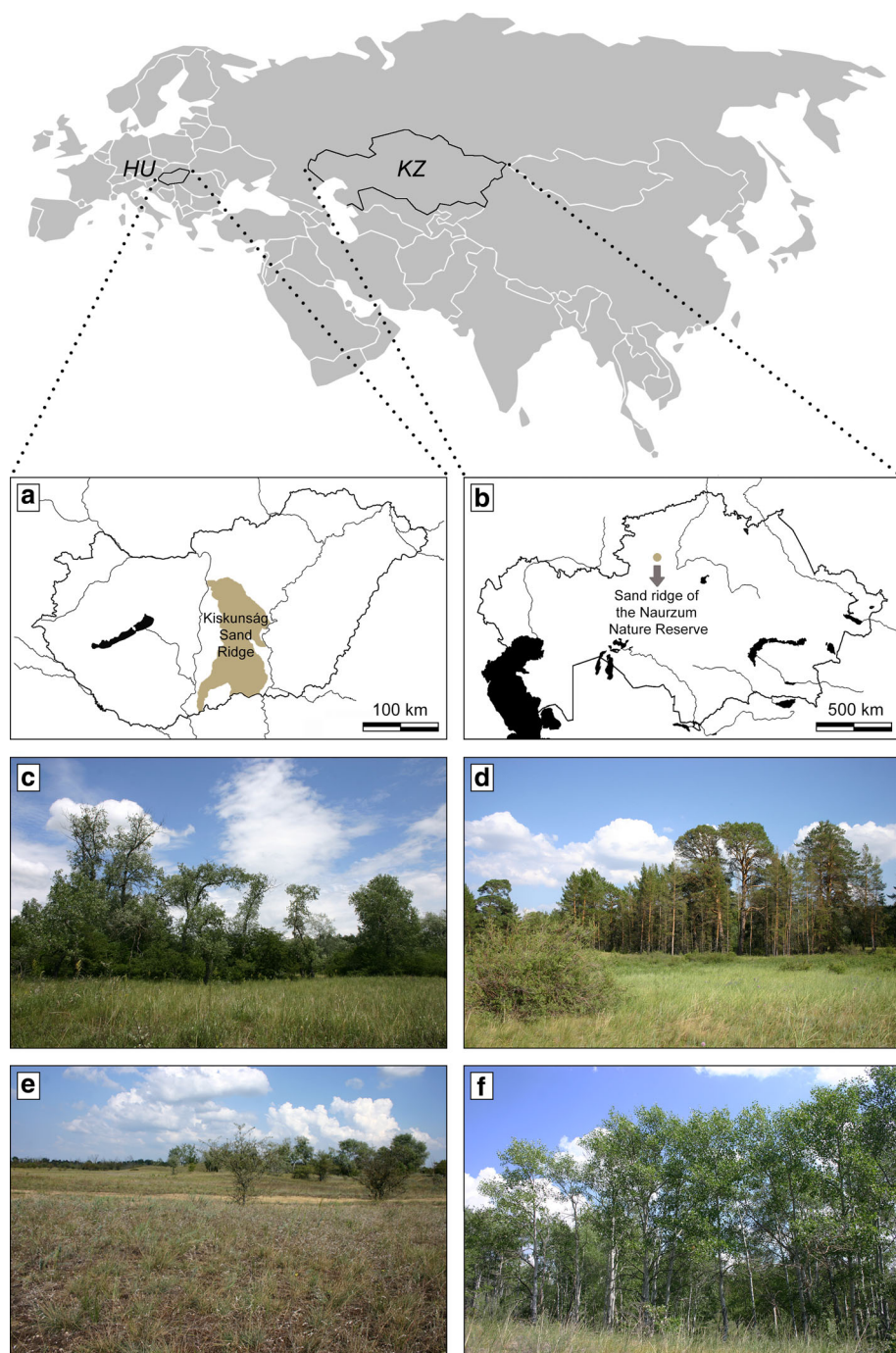


Fig. 1 Location of the study sites in Hungary (**a**) and Kazakhstan (**b**); a deciduous forest patch with *Populus alba* in Kiskunság (**c**); a coniferous forest patch with *Pinus sylvestris* in Naurzum (**d**); a xeric sandy grassland in Kiskunság (**e**); and a deciduous forest patch with *Populus tremula* in Naurzum (**f**)

continental, with a mean annual temperature of 3.6 °C (mean January and July temperatures were − 17.5 and 20.4 °C, respectively) and a mean annual rainfall of about 280 mm (mean summer rainfall was 107 mm) for the period 2005–2015 (climate data source: <http://rp5.ru>; for the town of Esil). Abundant species of the xeric grasslands within our sites were *Achillea micrantha*, *Artemisia campestris* subsp. *inodora*, *Calamagrostis epigejos*, *Carex supina*, *Festuca beckeri*, *Galium verum*, *Potentilla incana*, *Psephellus sibiricus*, *Scorzonera ensifolia*, *Stipa capillata* and *Stipa pennata* s.l., with a total vegetation cover of 50–75%. Forest patches have been continuously present throughout the Holocene (Hoffmann and Usoltsev 2001). These forests are dominated by either 15–25 m tall evergreen conifers (*Pinus sylvestris*), or 5–15 m tall deciduous trees such as *Betula pendula*, *B. kirghisorum* and *Populus tremula*, with 40–75% tree canopy cover. Deciduous forest patches are restricted to dune slacks, while coniferous patches usually occur on higher elevations, in a seemingly irregular pattern embedded in the steppe matrix. Dominant shrubs of the forest patches include *Rhamnus cathartica*, *Rosa acicularis* and *Spiraea hypericifolia*. Shrub cover is 0–75%. The most abundant species of the herb layer in the forests are *Agropyron cristatum* agg., *Artemisia pontica*, *Bromus inermis*, *Calamagrostis epigejos*, *Hierochloe odorata*, *Elymus repens* and *Lathyrus pratensis*.

Sampling

We studied three sites in both areas (1: N46°40', E19°27'; 2: N46°52', E19°24'; 3: N47°65', E19°23' in Kiskunság and 1: N51°32', E64°25'; 2: N51°31', E64°28', 3: N51°29', E64°27' in Naurzum), located at least 2 km from each other. We randomly selected three deciduous forest, three deciduous forest edge and three grassland plots in each site in both Kiskunság and Naurzum. Furthermore, three coniferous forest and three coniferous forest edge plots were also selected per each site in Naurzum. The average distance between two plots within a site was around 100 m. We selected large forest patches (> 0.5 ha) to minimise the confounding effect of edge influence in the forest interiors (cf. Murcia 1995). Forest edges were defined as the zones outwards from the outmost tree trunks, but still under the tree canopy. Since north-facing edges are expected to have the most distinct vegetation among differently oriented edges (Fraver 1994; Erdős et al. 2013a), only these ones were considered in the study.

The size of the grassland and forest plots was 5 × 5 m², while we used 2 × 12.5 m² plots in the edges for a better representation of the vegetation of these narrow microhabitats. Previous studies (Erdős et al. 2013a, 2014) suggested that plant species turnover at the forest edges of sandy forest-steppes varies along complex environmental gradients oriented both parallel and perpendicular to the axis of the edges; therefore, quadrat shape has no significant effect on vegetation descriptors in the present spatial scale (cf. Keeley and Fotheringham 2005). Our vegetation dataset contained a total of 72 (27 in Kiskunság and 45 in Naurzum) 25 m² plots, in which we recorded the percentage cover of all herbs, shrubs and tree saplings (with a height up to 50 cm).

Statistical analyses

To detect differences among the species composition of forest patches, edges and grasslands, detrended correspondence analysis (DCA, Hill and Gauch 1980) was carried out on the plots of the two areas (Kiskunság and Naurzum) based on the untransformed plant percentage cover data. Default number of segments (26) was used for detrending. Separate ordinations were carried out: (i) to characterise the habitat structure of the sandy forest-

steppe in Naurzum, including all plots of this area and (ii) to compare the habitat structure in Kiskunság and Naurzum, by focusing only on habitats that these areas share in common (deciduous forests, deciduous forest edges and grasslands). DCA ordinations were performed using the *vegan* package of R (R Development Core Team 2013; Oksanen et al. 2015).

Species frequencies and diagnostic plant taxa were determined for all habitat types in Naurzum, and for the deciduous forests, deciduous forest edges and grasslands in Kiskunság and Naurzum, respectively. The diagnostic value of each taxon for each habitat was calculated using the phi (Φ) coefficient as a measure of fidelity (Chytrý et al. 2002). The threshold value of Φ was 0.3. Non-diagnostic plant taxa were excluded with Fisher's exact test ($p < 0.05$). In the rare case when a species appeared to be diagnostic for two habitats, only the habitat with higher Φ value was considered. Calculations were done with the JUICE 7.0.25 program (Tichý 2002).

Plant taxa were classified into five groups (xerophilous sand, zonal steppe, meadow, forest and generalist species) according to their habitat preference (Király 2009; Komarov 1968–2002). All habitat types were characterised by the average plant cover belonging to the same group.

Species number, Shannon diversity and species evenness values were calculated for each plot in R environment. Linear mixed-effects models (LMMs) with Gaussian error term were built to reveal the effect of habitat type on these values. Site within the two study areas was included as a random variable. One LMM was built for the entire dataset of Naurzum, with five levels of habitat type (deciduous forest, deciduous forest edge, grassland, coniferous forest and coniferous forest edge), and another one jointly for the two study areas (Kiskunság and Naurzum), but including only those habitat types that occurred in both study areas (deciduous forest, deciduous forest edge and grassland). In the second set of LMMs, study area (Kiskunság and Naurzum) was also included as a second fixed factor besides habitat type and the interaction between the effects of study area and habitat type was also calculated. LMMs were built in R environment using the *lme* function of the *nlme* package (Pinheiro et al. 2015). Pairwise comparisons of the factor levels were assisted with the *relevel* function and primary p-values were corrected for multiple comparisons using the FDR (false discovery rate) method.

Nomenclature follows 'The Plant List' (www.theplantlist.org).

Results

Habitat structure and diversity patterns in Naurzum

The DCA revealed clear differences among the deciduous forests, coniferous forests and grasslands in Naurzum. However, deciduous forest edge plots were rather similar to deciduous forest and coniferous forest plots, while coniferous forest edge plots were scattered between grassland and coniferous forest plots (Fig. 2). Axis one opposed deciduous forest plots, on the left, and grassland plots, on the right. Among the deciduous forest and deciduous forest edge plots, there was a considerable variation, whereas grassland plots were more similar to each other.

Deciduous forests and grasslands had 15 diagnostic plant taxa each (equalling 29.4 and 46.9% of their species pool, respectively). The number of diagnostic plant taxa was similarly high in deciduous forest edges (14 plant taxa; 23.7% of the total species pool of

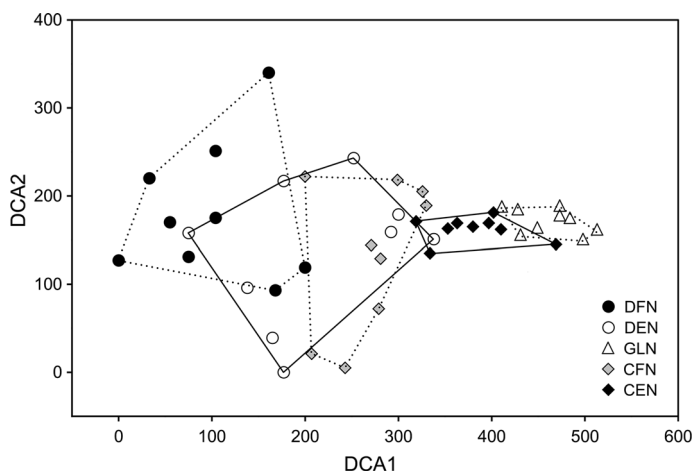


Fig. 2 DCA ordination diagram for the plots of Naurzum based on the untransformed plant percentage cover data. Default number of segments (26) was used for detrending. Eigenvalues were 0.76 and 0.43 for axis 1 and 2, respectively. Gradient length was 5.1 SD units for the first axis. *DFN* deciduous forest, *DEN* deciduous forest edge, *GLN* grassland, *CFN* coniferous forest, *CEN* coniferous forest edge

this habitat). However, there were only two diagnostic plant taxa in coniferous forests (6.7% of total species pool of this habitat) and two in coniferous forest edges (5.3% of total species pool of this habitat), respectively. The list of diagnostic plant taxa is given in Table 1.

The cover of xerophilous sand plants (e.g. *Bassia laniflora*, *Jurinea cyanoides* and *Scorzonera ensifolia*) was high in grasslands [average cover (%) of this species group was 55.2 ± 4.0 (mean \pm SE)] and coniferous forest edges (15.4 ± 2.8) and low in deciduous forests (1.7 ± 0.7). Zonal steppe plants (e.g. *Artemisia pontica*, *Festuca valesiaca* and *Thalictrum minus*) had a relatively high cover in all habitats (7.9 – 38.6 ± 1.3 – 7.5), with an especially high cover in deciduous forests (26.0 ± 5.7) and deciduous forest edges (38.6 ± 7.5), and the lowest cover in grasslands (7.9 ± 1.3). Meadow plants (e.g. *Artemisia dracunculus*, *Lathyrus pratensis* and *Tanacetum vulgare*) had a high cover in deciduous forests (12.3 ± 2.4), deciduous forest edges (14.9 ± 3.2) and coniferous forests (12.2 ± 4.1). The cover of forest plants (e.g. *Lithospermum officinale*, *Rhamnus cathartica* and *Rosa acicularis*) and generalists (e.g. *Calamagrostis epigejos*, *Chenopodium album* and *Elymus repens*) was the highest in deciduous forests (11.9 ± 6.2 and 19.0 ± 6.0 , respectively) (Fig. 3).

The highest species richness was found in the deciduous forest edges, while the lowest one was in the coniferous forests (Fig. 4, Table 2). Coniferous forests also had the lowest Shannon diversity values, while deciduous forests, deciduous forest edges and grasslands had similarly high values and coniferous forest edges were intermediate. Species evenness values showed no significant differences between any of the studied habitat types in Naurzum.

Table 1 Synoptic table of the sandy forest-steppe habitats (deciduous forests, deciduous forest edges, grasslands, coniferous forests and coniferous forest edges) in Naurzum with percentage frequency of diagnostic species (values in boldface)

Deciduous forests					
<i>Thalictrum minus</i>	33 ^{53.5}	—	—	—	—
<i>Rosa acicularis</i>	78 ^{50.4}	78 ^{50.4}	—	—	—
<i>Rhamnus cathartica</i>	56 ^{44.4}	44	—	—	—
<i>Salix rosmarinifolia</i>	22 ^{43.1}	—	—	—	—
<i>Lithospermum officinale</i>	22 ^{43.1}	—	—	—	—
<i>Lathyrus pratensis</i>	22 ^{43.1}	—	—	—	—
<i>Hieracium umbellatum</i>	22 ^{43.1}	—	—	—	—
<i>Iris</i> sp.	33 ^{42.9}	11	—	—	—
<i>Asparagus officinalis</i>	89 ^{42.3}	56	—	67	22
<i>Artemisia pontica</i>	67 ^{41.7}	56	—	22	—
<i>Populus tremula</i>	44 ^{39.9}	33	—	—	—
<i>Betula pendula</i>	44 ^{39.9}	33	—	—	—
<i>Adonis vologensis</i>	44 ^{39.9}	33	—	—	—
<i>Elymus repens</i>	56 ^{36.2}	33	—	11	22
<i>Tanacetum vulgare</i>	33 ^{35.4}	22	—	—	—
Deciduous forest edges					
<i>Poa pratensis</i> agg.	56	89 ^{66.2}	—	—	—
<i>Galatella</i> sp.	—	44 ^{62.5}	—	—	—
<i>Achillea setacea</i>	11	56 ^{62.1}	—	—	—
<i>Allium lineare</i>	44	100 ^{58.5}	—	33	33
<i>Festuca valesiaca</i>	22	67 ^{53.5}	—	11	11
<i>Veronica spuria</i>	44	89 ^{52.7}	—	22	33
<i>Galium verum</i>	22	89 ^{52.7}	22	22	33
<i>Equisetum hyemale</i>	67	89 ^{52.7}	—	22	11
<i>Rosa acicularis</i>	78 ^{50.4}	78 ^{50.4}	—	—	—
<i>Chondrilla brevirostris</i>	—	22 ^{43.1}	—	—	—
<i>Glycyrrhiza uralensis</i>	44	56 ^{40.1}	—	11	—
<i>Spiraea hypericifolia</i>	44	67 ^{38.4}	—	22	22
<i>Artemisia dracunculus</i>	22	33 ^{35.4}	—	—	—
<i>Hierochloa odorata</i>	67	89 ^{33.5}	33	78	11
Grasslands					
<i>Achillea micrantha</i>	—	11	100 ^{82.9}	—	22
<i>Potentilla incana</i>	—	—	89 ^{80.2}	—	22
<i>Psephellus sibiricus</i>	—	11	89 ^{75.0}	—	22
<i>Alyssum lenense</i>	—	—	56 ^{70.7}	—	—
<i>Jurinea cyanoides</i>	—	—	44 ^{62.5}	—	—
<i>Bassia laniflora</i>	—	22	78 ^{62.1}	—	22
<i>Scorzonera ensifolia</i>	—	44	100 ^{58.5}	11	56
<i>Festuca beckeri</i>	—	33	100 ^{53.5}	11	89 ^{42.3}
<i>Cleistogenes squarrosa</i>	—	—	44 ^{53.0}	—	11
<i>Gypsophila paniculata</i>	22	44	100 ^{46.8}	22	78
<i>Scorzonera</i> sp.	—	—	44 ^{45.8}	—	22

Table 1 continued

<i>Asperula graveolens</i> subsp. <i>danilewskiana</i>	–	–	22 ^{43.1}	–	–
<i>Stipa pennata</i> s.l./ <i>S. capillata</i>	22	67	100 ^{42.7}	11	89 ^{31.5}
<i>Eremogone procera</i>	–	11	44 ^{39.9}	–	22
<i>Artemisia campestris</i> subsp. <i>inodora</i>	–	44	67 ^{35.4}	–	56
Coniferous forests					
<i>Ephedra distachya</i>	–	–	–	33 ^{53.5}	–
<i>Ribes saxatile</i>	22	11	–	56 ^{49.4}	–
Coniferous forest edges					
<i>Pinus sylvestris</i>	–	11	–	56	100 ^{70.7}
<i>Koeleria glauca</i>	–	67	56	11	78 ^{36.0}

Within blocks of diagnostic species, species are ranked by decreasing fidelity ($\Phi \times 100$, superscript numbers). *Rosa acicularis* was diagnostic for two habitats

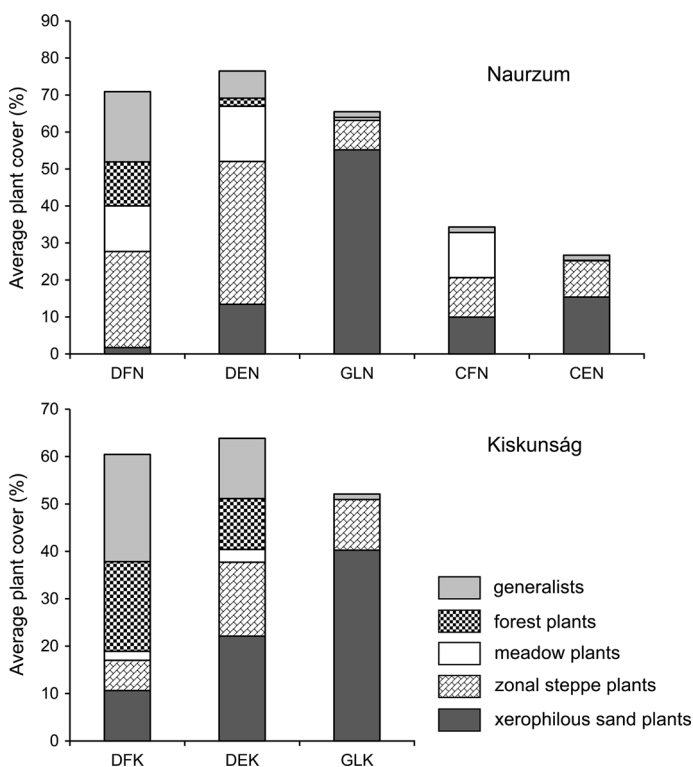


Fig. 3 Proportions of the habitat preference groups of the sandy forest-steppe habitats in Naurzum and Kiskunság. Naurzum: *DFN* deciduous forest, *DEN* deciduous forest edge, *GLN* grassland, *CFN* coniferous forest, *CEN* coniferous forest edge; Kiskunság: *DFK* deciduous forest, *DEK* deciduous forest edge, *GLK* grassland

Fig. 4 Species richness, Shannon diversity and species evenness of the sandy forest-steppe habitats in Kiskunság and Naurzum. Lower case letters indicate significant differences found with two separate linear mixed-effects models. One model was built for the five habitats in Naurzum (letters a–c) and another one for those habitats that Kiskunság and Naurzum have in common (letters i–l). Kiskunság: *DFK* deciduous forest, *DEK* deciduous forest edge, and *GLK* grassland; Naurzum: *DFN* deciduous forest, *DEN* deciduous forest edge, *GLN* grassland, *CFN* coniferous forest, and *CEN* coniferous forest edge

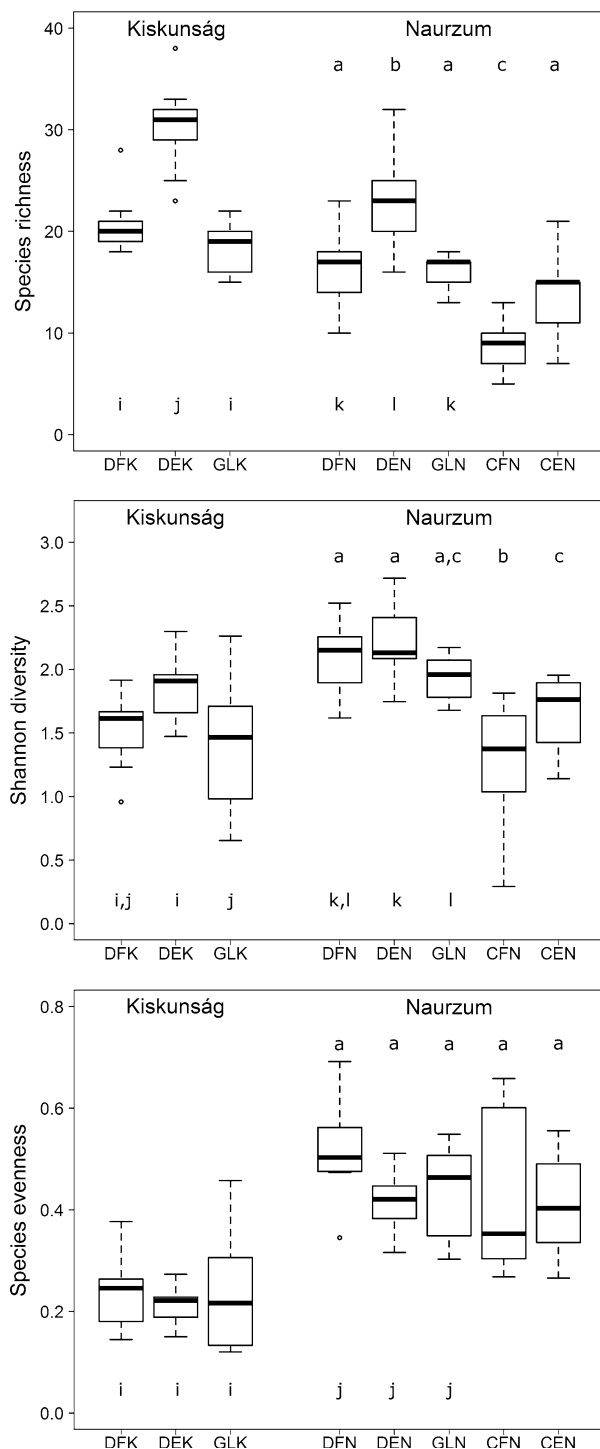


Table 2 Pairwise comparisons of the five habitat types of Naurzum based on linear mixed-effects models

	Species richness		Shannon diversity		Species evenness	
	t	p	t	p	t	p
CEN vs CFN	− 2.724	0.014	− 2.434	0.030	0.719	0.886
CEN vs DEN	5.771	< 0.001	3.509	0.003	0.165	0.886
CEN vs DFN	1.751	0.111	2.591	0.028	1.803	0.400
CEN vs GLN	1.621	0.127	2.065	0.066	0.574	0.886
CFN vs DEN	8.459	< 0.001	5.524	< 0.001	− 0.429	0.886
CFN vs DFN	4.474	< 0.001	4.606	< 0.001	1.209	0.588
CFN vs GLN	4.345	< 0.001	4.499	< 0.001	− 0.144	0.886
DEN vs DFN	− 4.021	< 0.001	− 1.109	0.306	1.981	0.400
DEN vs GLN	− 4.150	< 0.001	− 1.800	0.101	0.309	0.886
DFN vs GLN	− 0.130	0.898	− 0.882	0.384	− 1.329	0.588

Significant differences are indicated with boldface; p-values were corrected with the FDR method

DFN deciduous forest, *DEN* deciduous forest edge, *GLN* grassland, *CFN* coniferous forest, *CEN* coniferous forest edge

Comparison of the deciduous forest–grassland mosaics in Kiskunság and Naurzum

DCAs revealed similar patterns in Kiskunság and Naurzum, with a considerable overlap between deciduous forests and edges in the ordination space. However, grassland plots formed a distinct group along the first axis, and they were very similar to one another in both areas (Fig. 5).

The highest number of diagnostic plant taxa was found in the grasslands and the lowest in the forests both in Kiskunság (19 and 5 species, respectively) and Naurzum (15 and 2 species, respectively). The number of diagnostic plant taxa was intermediate in the edges (11 species in Kiskunság and 10 species in Naurzum) (see Supplementary Material Online Resources 1 and 2).

The cover of xerophilous sand plants was the highest in the grasslands in both areas [average cover (%) of this species group was 40.3 ± 3.6 (mean \pm SE) in Kiskunság]. Zonal steppe plants had the highest cover in the deciduous forest edges (15.6 ± 3.0 in Kiskunság); however, the cover of forest plants in Kiskunság (10.7 ± 4.3) and the cover of meadow plants in Naurzum were also considerable. The cover of forest plants and generalists was the highest in deciduous forests in both areas (18.9 ± 7.5 and 22.6 ± 6.8 in Kiskunság, respectively) (Fig. 3). The cover data of the species groups for the habitat types of Naurzum are given in the previous section.

Species richness was significantly higher in Kiskunság than in Naurzum. Among the three habitat types, deciduous forest edges were the most species rich, while grasslands and deciduous forests had lower values (Fig. 4, Table 3). Shannon diversity was higher in Naurzum than in Kiskunság. Edges tended to have a higher diversity than grasslands, while deciduous forests did not differ from the other habitat types in this respect. Study area had a significant effect on species evenness, with the higher values in Naurzum. Habitat type, however, had no detectable effect on evenness. Neither of the LMMs confirmed significant interactions between the explanatory variables (area and habitat type), indicating that the

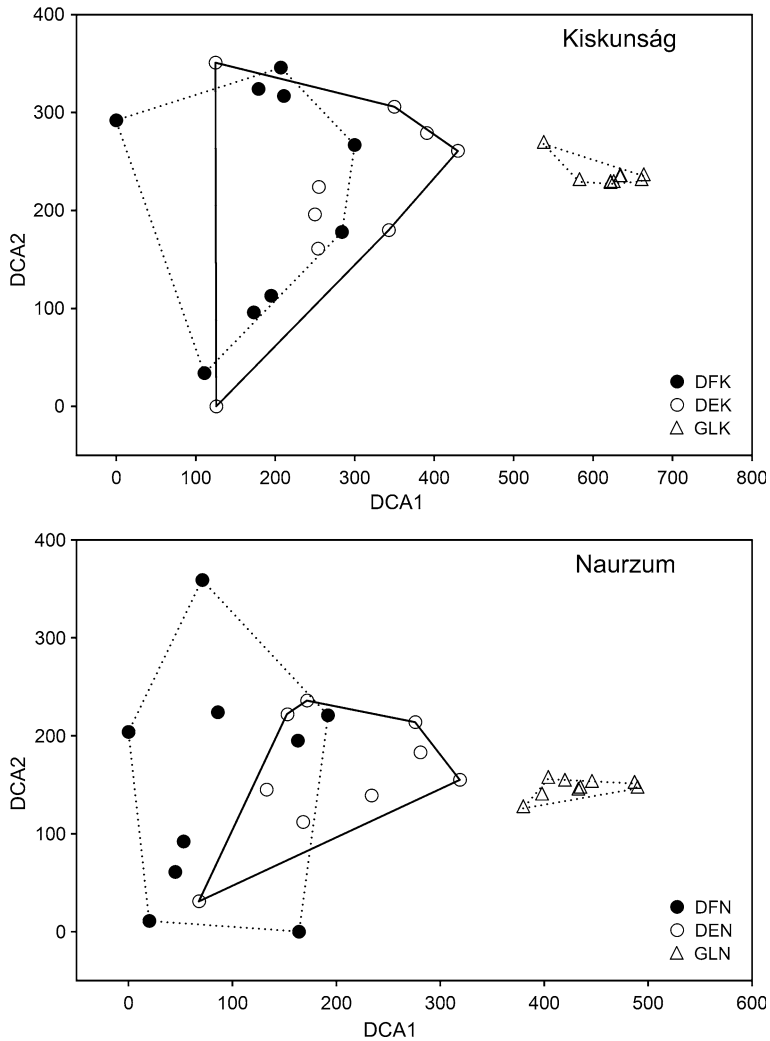


Fig. 5 DCA ordination diagrams for the plots of Kiskunság and Naurzum based on the untransformed plant percentage cover data. Default number of segments (26) was used for detrending. Axis 1 and 2 eigenvalues were 0.89 and 0.50 for Kiskunság, and 0.80 and 0.43 for Naurzum. Gradient length was 6.6 and 4.9 SD units for the first axis in Kiskunság and Naurzum, respectively. Kiskunság: *DFK* deciduous forest, *DEK* deciduous forest edge, *GLK* grassland; Naurzum: *DFN* deciduous forest, *DEN* deciduous forest edge, *GLN* grassland

relations of habitat types are largely independent of the area and the differences and similarities between the areas are largely independent of the habitat type (Table 3).

Table 3 Results of the linear mixed-effects models performed on the habitat types of Kiskunság and Naurzum

	Species richness		Shannon diversity		Species evenness	
	t	p	t	p	t	p
Area: habitat (DE and DF)	1.165	0.351	0.764	0.629	1.472	0.261
Area: habitat (DE and GL)	1.910	0.110	0.551	0.683	− 0.159	0.875
Area: habitat (DF and GL)	0.745	0.460	− 0.186	0.853	− 1.544	0.261
Kiskunság vs Naurzum	− 4.713	0.005	5.000	0.007	8.376	< 0.001
DE vs DF	− 6.825	< 0.001	− 2.324	0.058	2.102	0.144
DE vs GL	− 7.742	< 0.001	− 3.504	0.007	0.682	0.582
DF vs GL	− 0.916	0.426	− 1.244	0.385	− 1.320	0.271

The upper three data rows detail the interactions between areas (Kiskunság and Naurzum) and habitat (every pair formed from the three habitat types); the rest of the data belong to the main effects. Significant differences are indicated with boldface; p-values were corrected with the FDR method

DF deciduous forest, DE deciduous forest edge, GL grassland

Discussion

Despite the large geographical distance between the two investigated Eurasian sandy forest-steppes, their habitat structure and diversity patterns are similar and their components play important roles in the preservation of different groups of plant species. Our results also highlight the importance of forest edges as an integral component of this heterogeneous landscape and their role in maintaining landscape-scale diversity.

We found that the deciduous forest edges of both areas had higher species richness and Shannon diversity than the neighbouring habitats (Fig. 4). As indicated by the DCA ordinations (Fig. 5), their vegetation seems to be more similar to forest interiors than to grasslands, which is in line with some previous studies (e.g. Jakucs 1972; Mészáros 1990; Orczewska and Glista 2005). Thus, these edges may be regarded as parts of the forests in the studied habitat mosaic. However, it is important to point out that deciduous forest edges of the sandy forest-steppes are remarkably different from forest interiors in several respects. Their greater species richness and Shannon diversity, the high number of diagnostic species (Table 1) (Erdős et al. 2013a) and the habitat preference of their species (Fig. 3) indicate that forest interiors and edges could be regarded as separate vegetation units. Our findings are in line with earlier results conducted in sandy forest–grassland mosaics in Europe. For example, Molnár (1998) found that forest edges possess their own species that are rare or absent in forest interiors (i.e. edge-related species). Also, life-form spectra and abiotic parameters (e.g. air humidity, soil moisture and temperature) of forest edges proved to differ strongly from those of the forest interiors (Erdős et al. 2014). These studies, as well as some of our present findings suggest that deciduous forest edges form a well-defined component in the mosaics of the sandy forest-steppes in both Europe and Asia. Although species richness and Shannon diversity were significantly higher in coniferous forest edges than in coniferous forests, we did not find any significant differences between these edges and grasslands. The number of diagnostic species was very low both in coniferous forests and their edges. These results are in line with previous studies (Kelly and Connolly 2000; Fekete et al. 2014) which have shown that the number of

acidophilic species (i.e. diagnostic species of coniferous forests) in the continental xeric *Pinus sylvestris* forests on calcareous sands may be highly variable and these forests may also contain many xeric grassland species such as *Carex supina*, *Potentilla incana* and *Stipa capillata*.

Species richness was higher in Kiskunság than in Naurzum (Fig. 4). The explanation for this pattern is likely related to regional (e.g. macroclimate and biogeographical patterns) and local (e.g. human disturbances and vegetation history) factors. Increasing continentality to the east (decreasing temperature, shorter frost-free period, increasing aridity and higher intra- and inter-annual temperature variation) results in reduced species richness (Berg 1958; Zlotin 2002; Chibilyov 2002). As Hungary is near the western border of the forest-steppe biome, continentality is tempered by the Atlantic Ocean. In addition, the Atlantic and continental climate effects are further diversified by considerable Mediterranean influences (see climate data of the areas). Consequently, the Carpathian Basin, surrounded by the Alps, Carpathians and Dinarides is a biogeographically diverse region (Varga 1995), which allows for the coexistence of different floristic elements and therefore increases the species pool of forest-steppes (Molnár et al. 2012; Erdős et al. 2014). Within the forest-steppe zone, human influence tends to decrease when proceeding to the east, especially east of the Ural Mountains (Zlotin 2002; Chibilyov 2002), although edaphic forest-steppes are usually less affected by human activity throughout the biome (Smelansky and Tishkov 2012). However, the relatively high number of generalists (including several non-indigenous plants) in Kiskunság is likely due to the direct and indirect effects of human disturbance, including afforestation, canalisation, overgrazing, road and highway construction, and agricultural activity (cf. Molnár et al. 2012; Biró et al. 2013; Kelemen et al. 2016). In addition, despite the relatively long treeless period between the fifteenth and nineteenth centuries in Central Hungary (Erdős et al. 2015), the number of forest plants was also much higher in Kiskunság than in Naurzum (Fig. 3).

Despite the higher species richness in Kiskunság, Shannon diversity was higher in Naurzum (Fig. 4). This is due to the increased species evenness in Naurzum, which may correspond to some forms of disturbance. Disturbance often acts selectively on particular taxa, but its non-selective form may prevent competitive exclusion and therefore increase the species evenness in a community (Huston 1979; Cardinale et al. 2000). For example, fire has a great impact on the diversity patterns of terrestrial ecosystems, by potentially increasing the evenness of many taxa, including plants (Peltzer et al. 2000; Morrison 2002; Kembell et al. 2005). In Kazakhstan, millions of hectares of steppes burn every year, caused either by thunderstorms or humans (Kamp et al. 2016). Steppe and forest fires regularly occur in Naurzum (UNESCO nomination dossier of ‘Saryarka—Steppe and Lakes of Northern Kazakhstan’). Besides fire, grazing (Hartnett et al. 1996; Sankaran 2005) and climatic constraints (Hillebrand et al. 2008) may also be responsible for the observed patterns of species evenness via altering competition in the communities. However, further investigations are needed to more accurately determine the effects of different disturbance types on the diversity patterns of Eurasian forest-steppes.

Anthropogenic climate change poses a great threat to the biodiversity of steppe and forest-steppe ecosystems (Kamp et al. 2016). Species may respond to climate changes by range-shifting (Holt 1990; Chen et al. 2011) and by persisting in environmentally stable habitats (Willis et al. 2000; Bátori et al. 2017). Stable habitats buffered from environmental change (e.g. increased temperature and drought) are known as refugia (Ashcroft 2010). Paleoecological and biogeographical studies show evidence of such sites enabling the persistence of many taxa during past climate changes and suggest that refugia are likely to play important roles in facilitating species persistence under global warming

(Stewart et al. 2010; Bátori et al. 2014). For example, basins, local depressions and ravines may serve as refugia for cold-adapted species, or mesic sites surrounded by arid habitats for mesic species (Dobrowski 2010; Keppel et al. 2012; Bátori et al. 2017; McLaughlin et al. 2017). Our results show that the forest patches and forest edges of Eurasian sandy forest-steppes play important roles in preserving zonal steppe and meadow plants (e.g. *Asparagus officinalis*, *Galium verum* and *Hierochloa odorata*) that are adapted to relatively mesic conditions. If climate continues to warm, as expected (Solomon et al. 2007), many of these forest patches may not persist as refugia for these species over longer time scales (cf. Dulamsuren et al. 2010, 2014).

Forest-steppes are among the most vulnerable biomes due to extensive habitat loss and under-protection (Berg 1958; Hoekstra et al. 2005). For example, only 6.8% of the total forest-steppe vegetation has survived in Hungary (Molnár et al. 2012). However, the situation is much better in the central and eastern parts of the biome (Lavrenko and Karamysheva 1993; Zlotin 2002; Smelansky and Tishkov 2012), where larger forest-steppe areas have remained intact. Both investigated sandy forest-steppe areas presented a high diversity in terms of species composition and vegetation structure (Figs. 3, 4). The unique flora and vegetation of the studied sites have a high conservation value. In Kiskunság, many protected and/or endemic plant species occur both in the grasslands (e.g. *Dianthus serotinus*, *Iris humilis* and *Tragopogon floccosus*) and in the forest patches (e.g. *Cephalanthera rubra* and *Epipactis bugacensis*) and also in the forest edges (e.g. *Epipactis atrorubens*); (Erdős et al. 2013a, 2014). Almost all of these species have been placed on the Hungarian Red List (Király 2007). The forest patches in Naurzum provide habitat for an endemic tree species (*Betula kirghisorum*), which is listed in the Red Book of Kazakhstan (Rachkovskaya and Bragina 2012). *Adonis volgensis*, *Stipa pennata* s.l. and *Tulipa* spp. are also important from a conservation point of view. The remaining sandy-forest steppes are at risk of degradation or disappearance in the upcoming decades. The grassland component in Hungary is threatened by the invasion of *Asclepias syriaca* and *Robinia pseudoacacia* (Molnár et al. 2012; Kelemen et al. 2016) and the forest-component is often highly degraded or completely eliminated by human activities (Erdős et al. 2014). The temporal increase of fire frequency may threaten both the grasslands and forests in Naurzum (UNESCO nomination dossier of ‘Saryarka—Steppe and Lakes of Northern Kazakhstan’). Since edges cannot exist without intact forest and grassland patches, these processes have an impact on the diverse vegetation of edges as well. Therefore, improving our understanding of the factors and processes that affect these unique ecosystems is vital for establishing effective conservation strategies.

Our study provides baseline information on the species composition and habitat structure of the sandy forest-steppes in Kazakhstan. The results suggest that sandy forest-steppes are complex ecosystems within the temperate zone of Eurasia. Due to the special characteristics of this vegetation complex, we emphasize the conservation value of all components, including grasslands, forest patches and their edges. Determining the potential impacts of climate change and other drivers of degradation on these habitats allows their protection and the selection of the most appropriate conservation strategies.

Acknowledgements The supports of the Hungarian Scientific Research Fund (AK: OTKA PD 116200; BD: OTKA PD 115627; LE: OTKA PD 116114; OV: OTKA PD111807 and NKFI FK 124404; ZB: NKFI K 124796) are gratefully acknowledged. AK was funded by the MTA’s Post-Doctoral Research Program; BD and OV were funded by the Bolyai János Fellowship of the Hungarian Academy of Sciences, LE’s and OV’s work was supported by the National Youth Excellence Scholarship (NTP-NFTÖ-16-0623, NTP-NFTÖ-16-0107). BD and OV were supported by the ÚNKP-17-4-III-DE-160 and ÚNKP-17-4-III-DE-151 New National Excellence Program of the Ministry of Human Capacities. We express our gratitude to the

Kostanay State Pedagogical Institute and the Science-Research Centre of the Problems of Ecology and Biology of KSPI for their support during the period of research in Kazakhstan. We would like to thank Zsolt Péntes for his help in statistical analysis. Thanks to Karsten Wesche and an anonymous reviewer for their perceptive and helpful comments.

References

- Ashcroft MB (2010) Identifying refugia from climate change. *J Biogeogr* 37:1407–1413
- Bátori Z, Csiky J, Farkas T et al (2014) The conservation value of karst dolines for vascular plants in woodland habitats of Hungary: refugia and climate change. *Int J Speleol* 43:15–26
- Bátori Z, Vojtkó A, Farkas T et al (2017) Large- and small-scale environmental factors drive distributions of cool-adapted plants in karstic microrefugia. *Ann Bot London* 119:301–309
- Berg LS (1958) *Die geographischen Zonen der Sowjetunion*. I. Teubner, Leipzig
- Bilz M (2011) *Dianthus serotinus*. The IUCN Red List of Threatened Species 2011: e.T165217A5991480. <https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T165217A5991480.en>
- Biró M, Czúcz B, Horváth F et al (2013) Drivers of grassland loss in Hungary during the post-socialist transformation (1987–1999). *Landsc Ecol* 28:789–803
- Borhidi A, Kevéy B, Lendvai G (2012) Plant communities of Hungary. Akadémiai Kiadó, Budapest
- Cadenasso ML, Pickett STA, Weathers KC et al (2003) A framework for a theory of ecological boundaries. *Bioscience* 53:750–758
- Cardinale BJ, Nelson K, Palmer MA (2000) Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* 91:175–183
- Chen IC, Hill JK, Ohlemüller R et al (2011) Rapid range shifts of species associated with high levels of climate warming. *Science* 333:1024–1026
- Chibilyov A (2002) Steppe and forest-steppe. In: Shahgedanova M (ed) *The physical geography of northern Eurasia*. Oxford University Press, Oxford, pp 248–266
- Chytrý M (2012) Vegetation of the Czech Republic: diversity, ecology, history and dynamics. *Preslia* 84:427–504
- Chytrý M, Tichý L, Holt J et al (2002) Determination of diagnostic species with statistical fidelity measures. *J Veg Sci* 13:79–90
- Deák B, Tóthmérész B, Valkó O et al (2016) Cultural monuments and nature conservation: a review of the role of kurgans in the conservation and restoration of steppe vegetation. *Biodivers Conserv* 25:2473–2490
- Dengler J, Becker T, Ruprecht E et al (2012) Festuco-Brometea of the Transylvanian Plateau (Romania)—a preliminary overview on syntaxonomy, ecology and biodiversity. *Tuexenia* 32:319–359
- Dobrowski SZ (2010) A climatic basis for microrefugia: the influence of terrain on climate. *Glob Change Biol* 17:1022–1035
- Dubyna DV, Neuhauslová Z, Šeljag-Sosonko JR (1995) Vegetation of the Birjučij Island Spit in the Azov Sea. *Folia Geobot Phytotx* 30:1–31
- Dulamsuren C, Hauck M, Mühlenberg M (2005) Vegetation at the taiga forest–steppe borderline in the western Khentey Mountains, northern Mongolia. *Ann Bot Fenn* 42:411–426
- Dulamsuren C, Hauck M, Leuschner C (2010) Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. *Glob Change Biol* 16:3024–3035
- Dulamsuren C, Khishigjargal M, Leuschner C et al (2014) Response of tree-ring width to climate warming and selective logging in larch forests of the Mongolian Altai. *J Plant Ecol* 7:24–38
- Eliáš P, Sopotlieva D, Dítě D et al (2013) Vegetation diversity of salt-rich grasslands in Southeast Europe. *Appl Veg Sci* 16:521–537
- Erdős L, Gallé R, Bátori Z et al (2011) Properties of shrubforest edges: a case study from South Hungary. *Cent Eur J Biol* 6:639–658
- Erdős L, Cserhalmi D, Bátori Z et al (2013a) Shrub encroachment in a wooded-steppe mosaic: combining GIS methods with landscape historical analysis. *Appl Ecol Environ Res* 11:371–384
- Erdős L, Gallé R, Körmöczy L et al (2013b) Species composition and diversity of natural forest edges: edge responses and local edge species. *Community Ecol* 14:48–58
- Erdős L, Tölgyesi C, Horzse M et al (2014) Habitat complexity of the Pannonian forest-steppe zone and its nature conservation implications. *Ecol Complex* 17:107–118
- Erdős L, Tölgyesi C, Cseh V et al (2015) Vegetation history, recent dynamics and future prospects of a Hungarian sandy forest-steppe reserve: forest-grassland relations, tree species composition and size-class distribution. *Community Ecol* 16:95–105

- Ermakov N, Maltseva T (1999) Phytosociological peculiarities of South Siberian forest meadows. *Ann Bot* 57:63–72
- Fagan WF, Cantrell RS, Cosner C (1999) How habitat edges change species interactions. *Am Nat* 153:165–182
- Fekete G, Molnár Z, Magyari E et al (2014) A new framework for understanding Pannonian vegetation patterns: regularities, deviations and uniqueness. *Community Ecol* 15:12–26
- Feurdean A, Marinova E, Nielsen AB et al (2015) Origin of the forest steppe and exceptional grassland diversity in Transylvania (central-eastern Europe). *J Biogeogr* 42:951–963
- Fraver S (1994) Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. *Conserv Biol* 8:822–832
- Habel JC, Dengler J, Janišová M et al (2013) European grassland ecosystems: threatened hotspots of biodiversity. *Biodivers Conserv* 22:2131–2138
- Hartnett DC, Hickman KR, Walter LEF (1996) Effects of bison grazing, fire and topography on floristic diversity in tallgrass prairie. *J Range Manag* 49:413–420
- Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47–58
- Hillebrand H, Bennett DM, Cadotte MW (2008) Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89:1510–1520
- Hoekstra JM, Boucher TM, Ricketts TH et al (2005) Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecol Lett* 8:23–29
- Hoffmann CW, Usoltsev VA (2001) Modelling root biomass distribution in *Pinus sylvestris* forests of the Turgai Depression of Kazakhstan. *For Ecol Manag* 149:103–114
- Holt RD (1990) The microevolutionary consequences of climate change. *Trends Ecol Evol* 5:311–315
- Horvat I, Glavač V, Ellenberg H (1974) Vegetation Südosteuropas. Gustav Fischer, Stuttgart
- Huston M (1979) A general hypothesis of species diversity. *Am Nat* 113:81–101
- Ivanov A (2002) The Far East. In: Shahgedanova M (ed) The physical geography of northern Eurasia. Oxford University Press, Oxford, pp 422–447
- Jakucs P (1972) Dynamische Verbindung der Wälder und Rasen. Akadémiai Kiadó, Budapest
- Kamp J, Koshkin MA, Bragina TM et al (2016) Persistent and novel threats to the biodiversity of Kazakhstan's steppes and semi-deserts. *Biodivers Conserv* 25:2521–2541
- Keeley JE, Fotheringham CJ (2005) Plot shape effects on plant species diversity measurements. *J Veg Sci* 16:249–256
- Kelemen A, Valkó O, Kröel-Dulay G et al (2016) The invasion of common milkweed (*Asclepias syriaca* L.) in sandy old-fields—is it a threat to the native flora? *Appl Veg Sci* 19:218–224
- Kelly DL, Connolly A (2000) A review of the plant communities associated with Scots pine (*Pinus sylvestris* L.) in Europe, and an evaluation of putative indicator/specialist species. *For Syst* 1:15–39
- Kemball KJ, Wang GG, Dang QL (2005) Response of understory plant community of boreal mixedwood stands to fire, logging, and spruce budworm outbreak. *Can J Bot* 83:1550–1560
- Keppel G, Van Niel KP, Wardell-Johnson GW et al (2012) Refugia: identifying and understanding safe havens for biodiversity under climate change. *Glob Ecol Biogeogr* 21:393–404
- Király G (ed) (2007) Vörös Lista. A magyarországi edényes flóra veszélyeztetett fajai, Saját kiadás, Sopron
- Király G (ed) (2009) Új magyar fűvészkönyv. Magyarország hajtásos növényei, Aggteleki Nemzeti Park Igazgatóság, Jósza
- Király G, Stevanović V (2011) *Dianthus diutinus*. The IUCN red list of threatened species 2011: e.T161924A5514465. <https://doi.org/10.2305/IUCN.UK.2011-1.RLTS.T161924A5514465.en>
- Kolasa J, Zalewski M (1995) Notes on ecotone attributes and functions. *Hydrobiologia* 303:1–7
- Komarov VL (ed) (1968–2002) Flora of the U.S.S.R. Smithsonian Institution Libraries, Washington, DC
- Korotchenko I, Peregrym M (2012) Ukrainian steppes in the past, at present and in the future. In: Werger MJA, van Staalduinen MA (eds) Eurasian steppes. Ecological problems and livelihoods in a changing world. Springer, Dordrecht, pp 173–196
- Lavrenko EM (1969) Über die Lage des Eurasiatischen Steppengebiets in dem System der Pflanzen-geographischen Gliederung des Aussertropischen Eurasiens. *Vegetatio* 19:11–20
- Lavrenko EM, Karamysheva ZV (1993) Steppes of the former Soviet Union and Mongolia. In: Coupland RT (ed) Ecosystems of the world 8B. Natural grasslands, Eastern hemisphere and résumé, Elsevier, Amsterdam, pp 3–59
- Liu H, Yin Y, Wang Q et al (2015) Climatic effects on plant species distribution within the forest-steppe ecotone in northern China. *Appl Veg Sci* 18:43–49
- Magyari EK, Chapman JC, Passmore DG et al (2010) Holocene persistence of wooded steppe in the Great Hungarian Plain. *J Biogeogr* 37:915–935

- Mathar WP, Kämpf I, Kleinebecker T et al (2016) Floristic diversity of meadow steppes in the Western Siberian Plain: effects of abiotic site conditions, management and landscape structure. *Biodivers Conserv* 25:2361–2379
- McLaughlin BC, Ackerly DD, Klos PZ, Natali J, Dawson TE, Thompson S (2017) Hydrologic refugia, plants, and climate change. *Glob Change Biol*. <https://doi.org/10.1111/gcb.13629>
- Mészáros I (1990) Spatial changes in herb layer in a beech forest/clear-cut area ecotone from northern Hungary. In: Krahulec F, Agnew ADQ, Agnew S, Willems JH (eds) *Spatial processes in plant communities*. Academia, Prague, pp 59–69
- Molnár Z (1998) Interpreting present vegetation features by landscape historical data: an example from a woodland-grassland mosaic landscape (Nagykörös Wood, Kiskunság, Hungary). In: Kirby KJ, Watkins C (eds) *The ecological history of European forests*. CAB International, Wallingford, pp 241–263
- Molnár Z (2003) A Kiskunság száraz homoki növényzete. TermészetBÚVÁR Alapítvány Kiadó, Budapest
- Molnár Z, Biró M, Barthá S et al (2012) Past trends, present state and future prospects of Hungarian forest-steppes. In: Werger MJA, van Staalduinen MA (eds) *Eurasian steppes. Ecological problems and livelihoods in a changing world*, Springer, Dordrecht, pp 209–252
- Morrison DA (2002) Effects of fire intensity on plant species composition of sandstone communities in the Sydney region. *Austral Ecol* 27:433–441
- Müller P (1981) *Arealsysteme und Biogeographie*. Ulmer Verlag, Stuttgart
- Murcia C (1995) Edge effects in fragmented forests: implications for conservation. *Trends Ecol Evol* 10:58–62
- Novenko EY, Tsyganov AN, Rudenko OV et al (2016) Mid- and late-Holocene vegetation history, climate and human impact in the forest-steppe ecotone of European Russia: new data and a regional synthesis. *Biodivers Conserv* 25:2453–2472
- Odum EP (1971) *Fundamentals of Ecology*, 3rd edn. WB Saunders, Philadelphia
- Oksanen J, Blanchet FG, Kindt R et al (2015) *Vegan: community ecology*. <http://CRAN.R-project.org/package=vegan>
- Orczewska A, Glista A (2005) Floristic analysis of the two woodland-meadow ecotones differing in orientation of the forest edge. *Pol J Ecol* 53:365–382
- Parnikoza I, Vasiluk A (2011) Ukrainian steppes: current state and perspectives for protection. *Ann Univ Mariae Curie Skłodowska* 66:23–37
- Peltzer DA, Bast ML, Wilson SD et al (2000) Plant diversity and tree responses following contrasting disturbances in boreal forest. *For Ecol Manag* 127:191–203
- Peters DPC, Gosz JR, Pockman WT et al (2006) Integrating patch and boundary dynamics to understand and predict biotic transitions at multiple scales. *Landsc Ecol* 21:19–33
- Pianka ER (1983) *Evolutionary Ecology*, 3rd edn. Harper and Raw, New York
- Pinheiro J, Bates D, Debroy S et al (2015) R Development Core Team, nlme: linear and nonlinear mixed effects models. R package version 3.1–122. <http://CRAN.Rproject.org/package=nlme>
- R Development Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. <http://www.R-project.org>
- Rachkovskaya EI, Bragina TM (2012) Steppes of Kazakhstan: Diversity and present state. In: Werger MJA, van Staalduinen MA (eds) *Eurasian steppes. Ecological problems and livelihoods in a changing world*, Springer, Dordrecht, pp 103–148
- Risser PG (1995) The status of the science examining ecotones. *Bioscience* 45:318–325
- Sankaran M (2005) Fire, grazing and the dynamics of tall-grass savannas in the Kalakad-Mundanthurai Tiger Reserve, South India. *Conserv Soc* 3:4–25
- Schultz J (2005) *The ecozones of the world*. Springer, Berlin
- Shahgedanova M, Mikhailov N, Larin S et al (2002) The mountains of southern Siberia. In: Shahgedanova M (ed) *The physical geography of northern Eurasia*. Oxford University Press, Oxford, pp 314–349
- Shmida A, Ellner S (1984) Coexistence of plant species with similar niches. *Vegetatio* 58:29–55
- Smekalova T, Maslovky O, Melnyk V (2011) *Agropyron dasyanthum*. The IUCN Red List of Threatened Species 2011: e.T176502A7254702. <http://dx.doi.org/10.2305/IUCN.UK.2011-1.RLTS.T176502A7254702.en>. Accessed 08 January 2017
- Smelansky IE, Tishkov AA (2012) The steppe biome in Russia: Ecosystem services, conservation status, and actual challenges. In: Werger MJA, van Staalduinen MA (eds) *Eurasian steppes. Ecological problems and livelihoods in a changing world*, Springer, Dordrecht, pp 45–101
- Solomon S, Qin D, Manning M et al (eds) (2007) *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge and New York NY
- Stewart JR, Lister AM, Barnes I et al (2010) Refugia revisited: individualistic responses of species in space and time. *Proc R Soc B* 277:661–671

- Tichý L (2002) JUICE, software for vegetation classification. *J Veg Sci* 13:451–453
- UNESCO nomination dossier of ‘Saryarka—Steppe and Lakes of Northern Kazakhstan’. For inscription on the list of cultural and natural world heritage of UNESCO, pp 351
- Valkó O, Török P, Deák B et al (2014) Review: prospects and limitations of prescribed burning as a management tool in European grasslands. *Basic Appl Ecol* 15:26–33
- van der Maarel E (1990) Ecotones and ecoclines are different. *J Veg Sci* 1:135–138
- Varga Z (1995) Geographical patterns of biological diversity in the Palaeartic Region and the Carpathian Basin. *Acta Zool Acad Sci H* 41:71–92
- Vicherek J (1972) Die Sandpflanzengesellschaften des unteren und mittleren Dnejrstromgebietes (die Ukraine). *Folia Geobot Phytotx* 7:9–46
- Walter H, Breckle SW (2002) *Walter’s Vegetation of the Earth*, 4th edn. Springer, Berlin
- Wesche K, Ambarlı D, Kamp J et al (2016) The Palaeartic steppe biome: a new synthesis. *Biodivers Conserv* 25:2197–2231
- Wiens JA, Crawford CS, Gosz JR (1985) Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421–427
- Willis KJ, Rudner E, Sümegi P (2000) The full-glacial forests of Central and southeastern Europe. *Quat Res* 53:203–213
- Zhang JT, Ru W, Li B (2006) Relationships between vegetation and climate on the loess plateau in China. *Folia Geobot* 41:151–163
- Zlotin R (2002) Biodiversity and productivity of ecosystems. In: Shahgedanova M (ed) *The physical geography of northern Eurasia*. Oxford University Press, Oxford, pp 169–190
- Zólyomi B, Fekete G (1994) The Pannonian loess steppe: differentiation in space and time. *Abstr Bot* 18:29–41