Tuexenia 39: 357–375. Göttingen 2019.
doi: 10.14471/2019.39.007, available online at www.zobodat.at

Trends in species composition and richness along a centre-to-periphery gradient in forest-steppes of the southern Carpathian Basin

Trends in Artenzusammensetzung und -reichtum von Waldsteppen entlang eines Zentrum-zur-Peripherie-Gradienten im südlichen Karpatenbecken

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Abstract

As a transitional zone between forests and steppes, the forest-steppe belt is thought to exhibit steep latitudinal vegetation changes. However, earlier studies have focused on only one habitat type, disregarding forest-steppe heterogeneity. We examined the compositional and species richness trends along a centre-to-periphery gradient in Hungary, across multiple habitats. We also investigated abiotic environmental factors, such as climate, soil, and land-use history, which potentially underlie the observed vegetation phenomena. The effects of the gradient on the overall species richness and the richness of different species groups were studied using generalized linear models. Changes in species composition and environmental variables along the gradient were analysed using detrended correspondence analysis. There was an apparent increase in species richness in some habitats, although different species groups reacted differently along the gradient. Furthermore, there was a well-defined compositional turnover, which was associated with a change in climatic, soil, and land-use variables. The marked trends in species composition and richness may be explained by the transitional nature of forest-steppes, where many species may be close to their tolerance limits. Ongoing global warming may entail a significant decrease in species richness. However, this decrease may be mitigated by protecting the diversity of habitats and species groups, as some of them will better withstand increasing aridity. Preserving forest-steppe integrity may thus be understood as an insurance policy.

Keywords: ecological complexity, forest-grassland mosaic, habitat heterogeneity, wooded-steppe

Erweiterte deutsche Zusammenfassung am Ende des Artikels

Manuscript received 9 October 2018, accepted 27 February 2019
Co-ordinating Editor: Viktoria Wagner

1. Introduction

Forest-steppes are among the most complex ecosystems in the northern temperate zone (WALTER & BRECKLE 1989, SCHULTZ 2005, ERDŐS et al. 2018a). As a tension zone between closed forests and treeless steppes, Eurasian forest-steppes extend from eastern Central Europe to the Russian and Chinese Far East and cover an area of 2.9 million km^2 (WESCHE et al. 2016). They are characterized by high biodiversity (ZLOTIN 2002, ERDŐS et al. 2018a) and a remarkable number of endemics, IUCN red-listed species, and other species of special conservation importance (CHIBILYOV 2002). Compared to other non-tropical biomes, forest-steppes have high net primary production (ZLOTIN 2002) and considerable carbon sequestration capacity (MÜLLER 1981, SCHULTZ 2005). Since forest-steppes are often used as pastures, they also have economic and cultural significance (SMELANSKY & TISHKOV 2012).

Forest-steppes (together with steppes) belong to the most threatened biomes on Earth (HOEKSTRA et al. 2005). Vast areas of forest-steppes, especially those in Europe, have been converted to arable land (TISHKOV 2002). At the same time, the number of legally protected forest-steppes is insufficient and consists largely of small and disconnected areas (SMELANSKY & TISHKOV 2012). Efficient nature conservation is usually hindered by knowledge gaps regarding the patterns and processes in forest-steppes (BONE et al. 2015, ERDŐS et al. 2018a). For example, our understanding of spatial heterogeneity, together with its causes and consequences, is incomplete. At the same time, climate change is likely to pose new challenges for the remaining forest-steppes (MOLNÁR et al. 2012, KAMP et al. 2016).

Spatial heterogeneity is manifested at several scales in forest-steppes (ERDŐS et al. 2018a). At the local scale, a number of different habitats (differently sized forest and grassland patches of numerous types and the edges between them), characterized by unique sets of structural, compositional and functional features, occur in close proximity (MOLNÁR 1998, BORHIDI et al. 2012, ERDŐS et al. 2014, 2015). Additionally, regional gradients are superimposed on these local patterns. For example, latitudinal gradients of aridity cause salient changes in vegetation even within relatively short distances (BERG 1958, CHIBILYOV 2002, FEKETE et al. 2010).

The westernmost Eurasian forest-steppes can be found in the Carpathian Basin (FEKETE et al. 2002, MAGYARI et al. 2010). This region shows a circular zonality due to its special biogeographical position (located at the contact zone of different vegetation belts and surrounded by mountain chains in virtually every direction). The outermost areas of the basin are covered by closed deciduous forests, the middle zone is occupied by forest-steppes, while the innermost zone is covered by steppe. To what extent the latter is natural vegetation is debated (MOLNÁR et al. 2012, SÜMEGI et al. 2012, FEKETE et al. 2014).

Several scientific studies have investigated the vegetation gradients extending from the centre to the periphery in the Carpathian Basin. For example, it has been shown that the overall per plot species richness and the local species pool of forest-steppe grasslands increases towards the periphery (KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2011). However, other habitat types of forest-steppes have been disregarded; thus, it is unknown whether a similar gradient is observable in other habitats such as forest interiors and edges. Moreover, most earlier studies have focused either on overall species richness, or on the richness of grassland-related specialist species, while other phytocoenological groups have largely been neglected (e.g. FEKETE et al. 2008, BARTHA et al. 2011). In addition, the factors underlying the vegetation gradient are not fully understood. Decreasing aridity from the centre to the periphery is usually assumed to be of primary importance (KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2008, 2011). However, soil characteristics (KOVÁCS-LÁNG et al. 2000), land-use

histories (BARTHA et al. 2008) and the geographical distances from the hilly and mountainous regions (FEKETE et al. 2010) may also have important effects on the coarse-scale patterns of species composition and species richness.

Our aim was to characterize the centre-to-periphery gradient in multiple forest-steppe habitats (large, medium and small forest patches, north-facing forest edges, south-facing forest edges, and open perennial grasslands). More specifically, our questions were as follows: (1) How do overall species richness and the species richness of different phytosociological preference groups change? (2) Do species composition and selected environmental variables shift?

2. Material and methods

2.1 Study area

We selected five sites ranging from the central to the southern (more peripheral) parts of the Danube-Tisza Interfluve (Hungary). Criteria during site selection were as follows: (1) sites had to be under legal protection, representing a near-natural state of sandy vegetation, and (2) sites had to be distributed as evenly as possible along the centre-to-periphery gradient. The five sites (from north to south) are as follows: Fülöpháza (Site A: N 46°52', E 19°25'), Bócsa (Site B: N 46°41', E 19°27'), Pirtó (Site C: N 46°28', E 19°26'), Kéleshalom (Site D: N 46°23', E 19°20'), and Négyestelep (Site E: N 46°17', E 19°35'). The total spatial length of the gradient is approximately 70 km (Fig. 1).

The mean annual temperature of the study sites is approximately 10.8 °C, and the mean annual precipitation varies between 530 and 570 mm (DÖVÉNYI 2010). The study sites are characterized by stabilized calcareous sand dunes and interdune depressions; the soils are humus-poor sandy soils with low water retention capacities (VÁRALLYAY 1993).

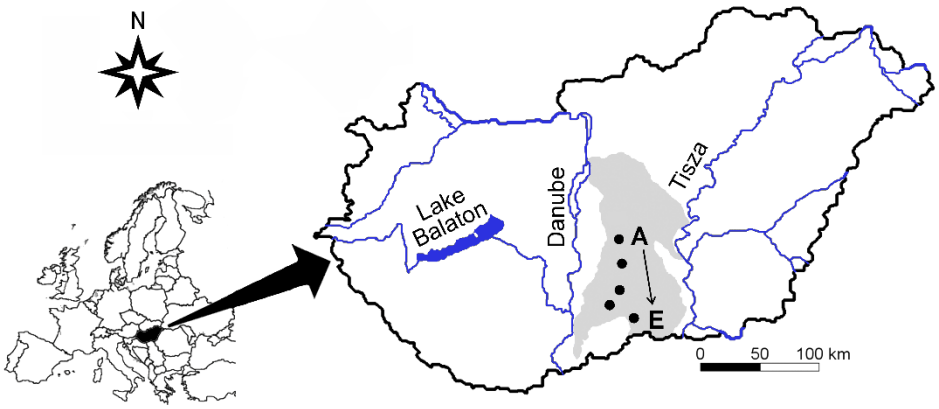


Fig. 1. The location of the study sites in Hungary between the Danube and Tisza Rivers from the centre (Site A) towards the periphery (Site E) of the Carpathian basin. Areas covered by calcareous sand dunes are indicated in grey (based on TÖLGYESI et al. 2016).

Abb. 1. Die Lage der Untersuchungsorte im Donau-Theiß Zwischenstromland (Ungarn) von der Mitte (A) zur Peripherie (E) des Karpatenbeckens. Gebiete mit kalkhaltigen Sanddünen sind grau markiert (basierend auf TÖLGYESI et al. 2016).

The natural vegetation of the sites is a mosaic of woody and herbaceous patches. The forest component is represented by juniper-poplar forests (*Junipero-Populetum albae* (Zólyomi ex Soó 1950) Szodfridt 1969). The canopy layer has usually a cover of 40–60% and is co-dominated by *Populus alba* and *P.* × *canescens*. In the shrub layer, *Juniperus communis* and *Crataegus monogyna* are the most frequent and abundant taxa. The most common species of the herb layer include *Anthriscus cerefolium*, *Asparagus officinalis*, *Carex flacca*, *C. liparicarpos*, *Poa angustifolia*, and *Stellaria media*. Where canopy and shrub covers are sparse, additional herb species occur, notably some xeric ones such as *Eryngium campestre*, *Festuca rupicola*, *Potentilla arenaria*, and *Taraxacum laevigatum* agg.

Open perennial sand grassland (*Festucetum vaginatae* Rapaics ex Soó 1929 em. Borhidi 1996) is the most widespread habitat among grassland communities, across all study sites. Dominant species are *Festuca vaginata*, *Stipa borysthenica*, and *S. capillata*, while *Alkanna tinctoria*, *Dianthus serotinus*, *Euphorbia seguieriana*, *Fumana procumbens*, *Poa bulbosa*, and *Secale sylvestre* are also common. The cryptogamous layer (e.g. *Cladonia foliacea* and *Syntrichia ruralis*) covers a considerable proportion of the surface. The bare sand cover can be as high as 50–60%.

Currently, all study sites are found in a landscape dominated by non-native forest plantations, ploughlands, fallow lands, settlements and farm buildings. Detailed information on the vegetation of the region can be found in BIRÓ et al. (2007, 2008) and BORHIDI et al. (2012).

The plant species names follow KIRÁLY (2009), and the plant community names are used according to BORHIDI et al. (2012).

2.2 Field sampling

Our previous research in similar forest-steppe ecosystems (ERDŐS et al. 2015, 2018b) revealed markedly different vegetation types. In line with these studies, we differentiated the following six habitat types at each study site: large forest patches (> 0.5 ha), medium forest patches (0.2–0.4 ha), small forest patches (< 0.1 ha), north-facing forest edges, south-facing forest edges, and open perennial grasslands. In this study, an edge was defined as the zone outside of the outermost tree trunks of a forest patch but still below the canopy. Earlier studies have shown that edges in the studied ecosystem are sharp and narrow (ERDŐS et al. 2015, 2018b). Vegetation was sampled using 25 m^2 plots. This plot size was selected because it was large enough to sample vegetation but small enough to study forest edges and small patches. Plots were 5 m × 5 m, except for the edge plots, which were adapted to the elongated edge habitats (to ensure that the plots did not extend into forest or grassland interiors) and were 2 m × 12.5 m. Earlier studies suggested that plot shape has no distorting effects on the results at this scale (KEELEY & FOTHERINGHAM 2005, BÁTORI et al. 2018). Plots were distributed within a circle of 1 km radius at each site. Plot midpoints were randomly placed within each habitat, but degraded areas were excluded from the study. Our aim was to have 150 plots (5 study sites × 6 habitats × 5 replicates), but the lack of availability of large forest patches reduced the number of replicates at sites C and D, resulting in a total of 144 plots. The percent cover of each vascular plant species in each vegetation layer was estimated in the plots in April and July 2016 (BRAUN-BLANQUET 1964).

2.3 Environmental variables

We analyzed how environmental variables changed along the centre-to-periphery-gradient and tested how they varied with species richness. Data on macroclimate (mean summer precipitation and mean summer temperature) was derived from the CarpatClim Database (www.carpatclim-eu.org; 0.1°spatial and 1 day temporal resolution). After aggregation to monthly temporal resolution and averaging in the period of 1977–2006, the data were downscaled to a 700 m resolution grid by SOMODI et al. (2017). We used summer months (June–August) in our analysis because semi-dry conditions during this period seem to have major limiting effects on vegetation (BORHIDI et al. 2012).

Furthermore, we derived soil parameters (sand fraction, $CaCO_3$ content, pH, organic matter content, water content at field capacity) from digital soil property maps elaborated in the frame of the DOSoReMI.hu initiative (dosoremi.hu; PÁSZTOR et al. 2017, 2018). We derived data from maps created with 100 m spatial resolution for the 0–30 cm soil layers and calculated mean values for 1 km circles around each site.

Land-use history and current landscape context were similarly studied in 1 km radius circles. For the 18th century, we acquired the prevailing habitat types from the reconstructed habitat map of the region (BIRÓ 2003) based on the First Military Survey of 1782–1785 (HM HIM). For the 19th century, the Second Military Survey (HM HIM 2005) was georeferenced, and landscape types were digitized. The current habitat map was based on BIRÓ et al. (2006) and the most recent satellite images available in ArcGIS 10.1 (online basemaps/imagery). Four categories were used: natural mosaic (natural or near-natural forest-steppe mosaic consisting of woody and grassland patches), dry sand grassland (with woody cover below 10%), other grassland (marshes, mesic grasslands, wetlands, fens, alkaline habitats), and anthropogenic habitat (ploughlands, vineyards, orchards, abandoned fields, settlements, gardens, infrastructure, tree plantations). The habitat maps of the sites are shown in Supplement E1. ArcGIS version 10.1 (ESRI) and QGIS version 2.0.1 software were used to prepare the data on climate, soil, and land-use history.

2.4 Data analyses

We calculated species richness for both native (S_{nat}) and adventive (non-native) (S_{adv}) species, as well as for species richness of phytosociological groups ($S_{grassland}$, S_{sand}, S_{forest}, S_{weed}, S_{indiff}) per plot. The latter indices were derived by assigning species according to their phytosociological preferences to groups defined by BORHIDI (1995). To reduce the number of categories, the following groups were used: (1) species of xeric grasslands (*Festuco-Brometea*, *Festucetalia valesiacae*, *Festucion valesiacae*, *Sedo-Scleranthetea*, *Sedo-Scleranthetalia*, *Alysso-Sedion*, *Corynephoretalia*, *Festuco-Sedetalia*) ($S_{grassland}$), (2) species strongly related to open sandy grasslands (*Festucetalia vaginatae*, *Festucion vaginatae*, *Bromion tectorum*) (S_{sand}), (3) species of forests, edges and scrubs (*Querco-Fagetea*, *Quercetea pubescentis-petraeae*, *Aceri tatarico-Quercion*, *Prunetalia spinosae*, *Trifolio-Geranietea*, *Geranion sanguinei*) (S_{forest}), (4) species of weed communities (*Chenopodietea*, *Polygono-Chenopodietalia*, *Secalietea*, *Secalietalia*, *Arction lappae*, *Calystegietalia*, *Glechometalia*, *Onopordion acanthii*, *Dauco-Melilotion*) (S_{weed}), (5) indifferent species (i.e., species without clear phytocoenological preferences, usually occurring in several different plant associations) (S_{indiff}), and (6) others (*Molinio-Arrhenatheretea*, *Molinietalia*, *Artemisio-Festucetalia*). As group 6 contained only five species that were very rare in the study plots, this group was not analysed (see Supplement E2 for species lists in each group).

We investigated the effect of habitat type and the centre-to-periphery gradient on species richness in species groups. We defined the centre-to-periphery gradient as a latitudinal distance of sites from the Fülöpháza site, located at the centre of the Carpathian Basin. We applied Poisson generalized linear models (GLMs) with habitat type treated as a categorical explanatory variable and latitudinal distance as a continuous explanatory variable. We tested for a linear latitudinal trend in the richness of species groups in the different habitat types. We specified model formulas to estimate a separate centre-to-periphery gradient slope coefficient for each habitat type (instead of an overall slope estimate). Statistical analyses were performed in the R environment (version 3.4.3) (R CORE TEAM 2017) by using the lme4 package (BATES et al. 2015). Models were checked for heteroscedasticity by visual inspection of diagnostic plots and tested for overdispersion with the dispersion test function of the AER package (KLEIBER & ZEILEIS 2008). In the case of overdispersion, we corrected the standard errors using a quasi-Poisson GLM.

To gather information on species richness at the site scale, we also computed the total number of native species in each habitat at each site by combining all corresponding study plots.

We used detrended correspondence analysis (DCA) (HILL & GAUCH 1980) to study compositional similarity of plots. The analysis used presence-absence data of native species and was performed in the vegan package (OKSANEN et al. 2018), in R. The DCA was run with four rescaling cycles and 26 segments (default values) in rescaling. We fit our environmental variables (Supplement E3) and the latitudinal distance of sites from the centre of the Carpathian Basin onto the DCA ordination space by finding the directions in which the variables changed most rapidly (i.e., maximal correlations). Significance and goodness of fit were calculated using 1000 permutations. In the DCA biplot, only five variables

with the highest correlations to the axes (i.e., square root of the goodness of fit) were displayed. Furthermore, we calculated a pairwise correlation matrix to investigate the relationship among environmental variables (Supplement E4).

3. Results

3.1 Species richness trends

We found a total of 219 species (198 native, 21 adventive) in 144 studied plots. The richness of native species (S_{nat}) per plot increased significantly from the centre towards the periphery in small forest patches, north-facing edges, and south-facing edges (Fig. 2a, Table 1). S_{nat} increased slightly in grasslands, but the trend was not significant. The richness of adventives (S_{adv}) increased significantly towards the periphery in large forest patches, south-facing edges and grasslands, while there was no significant trend in the other habitats (Fig. 2b, Table 1). The richness of xeric grassland species ($S_{grassland}$) increased significantly towards the periphery in small forest patches and north-facing edges (Fig. 2c, Table 1). The richness of sand grassland species (S_{sand}) increased towards the periphery only in north-facing edges (Fig. 2d, Table 1). While the richness of forest-related species (S_{forest}) did not show significant linear trends in any habitat (Fig. 2e, Table 1), the richness of weeds (S_{weed}) rose in all habitats towards the periphery (Fig. 2f, Table 1). The richness of indifferent species (S_{indiff}) increased only in south-facing edges and grasslands (Fig. 2g, Table 1).

When plots were pooled within each habitat for all sites separately, there was an increase in the number of species from the centre to the periphery for most habitats (Table 2).

3.2 Trends in species composition and environmental variables

Plots were separated according to habitat type along DCA axis 1 (gradient length: 3.936) (Fig. 3). Three well-defined groups emerged: the most distinct group was formed by grassland plots, the second group consisted of small forest patches, north-facing edges and south-facing edges, while large and medium forest patches appeared in the third group.

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Fig. 2. Per plot richness (mean ±SE) of (a) native and (b) adventive species, (c) dry grassland species, (d) sand grassland species, (e) forest species, (f) weeds, and (g) indifferent species across habitats along the studied gradient. To improve clarity, error bars were slightly shifted horizontally within each category. The sites are from north to south as follows: A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep. Lines are simple links of mean values. A statistical analysis of the underlying data is presented in Table 1.

Abb. 2. Artenreichtum (Mittelwert ±SE) von (a) einheimischen und (b) adventiven Arten sowie von (c) Trockerasenarten, (d) Sandrasenarten, (e) Arten der Wälder, (f) Arten von Unkrautgesellschaften, und (g) indifferenten Arten in den Lebensräumen entlang des untersuchten Gradienten. Die Fehlerbalken wurden horizontal leicht verschoben um die Lesbarkeit zu verbessern. Die Untersuchungsorte sind von Norden nach Süden: A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep. Die Linien stellen einfache Verbindungen der Mittelwerte dar. Eine statistische Analyse der zugrundeliegenden Daten ist Tabelle 1 zu entnehmen.

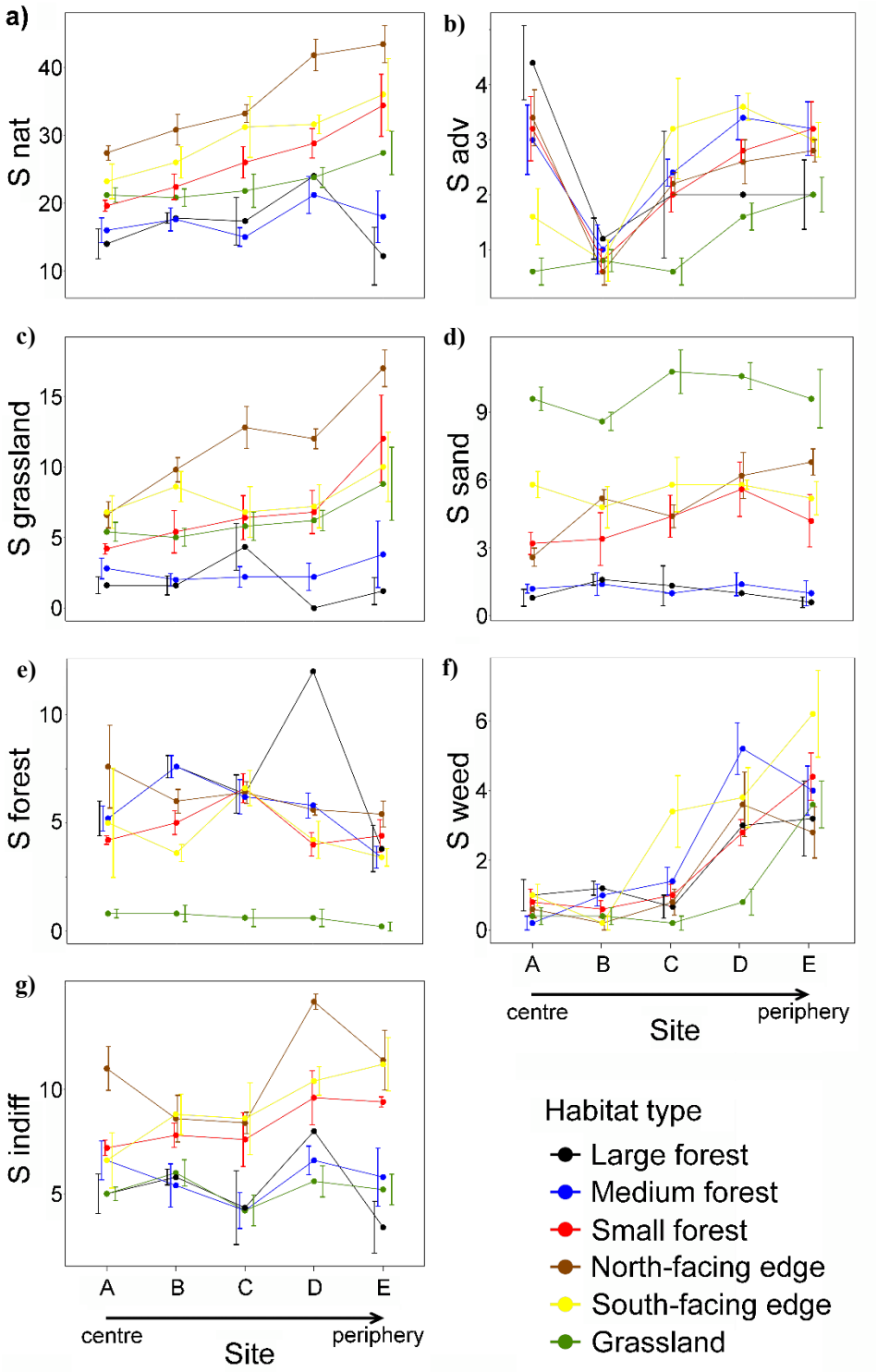

a)
S nat
40
30
20
10
b)
S adv
4
3
2
1
c)
S grassland
15
10
5
0
d)
S sand
9
6
3
0
e)
S forest
10
5
0
f)
S weed
6
4
2
0
g)
S indiff
10
5
A
B
C
D
E
centre
periphery
Site
Habitat type
Large forest
Medium forest
Small forest
North-facing edge
South-facing edge
Grassland

Table 1. Results of the Poisson GLMs for species richness in coenological species groups. Slope estimates (β), t-statistics and corresponding p values show if there is a significant linear trend in species richness in response to the centre-to-periphery gradient in each habitat type. S_{nat}: native species, S_{adv}: adventive species, $S_{grassland}$: dry grassland species, S_{sand}: sand grassland species, S_{forest}: forest species, S_{weed}: weed species, S_{indiff}: indifferent species; LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands.

Tabelle 1. Ergebnisse der Poisson GLMs des Artenreichtums der zoenologischen Artengruppen. Die Steigung (β), die t-Statistik und der entsprechende p-Wert zeigen, ob ein signifikanter linearer Trend des Artenreichtums in Abhängigkeit zum Zentrum-Peripherie Gradienten in den einzelnen Habitaten vorhanden ist. S_{nat}: einheimisceh Arten, S_{adv}: adventive Arten, $S_{grassland}$: Arten von Trockenrasen, S_{sand}: Arten von Sandrasen, S_{forest}: Waldarten, S_{weed}: Arten von Unkrautgesellschaften, S_{indiff}: indifferente Arten; LF: große Waldflächen, MF: mittelgroße Waldflächen, SF: kleine Waldflächen, NE: Waldränder mit nördlicher Ausrichtung, SE: Waldränder mit südlicher Ausrichtung, G: Grasland.

	Snat			Sadv			Sgrassland			Ssand			Sforest			Sweed			Sindiff		
	β	t	*p*	β	t	*p*	β	t	*p*	β	t	*p*	β	t	P	β	t	*p*	β	t	*p*
LF	-0.0001	0.355	0.724	-0.0119	1.961	0.050	0.0000	0.003	0.997	-0.0044	0.497	0.619	-0.0025	0.677	0.498	0.0194	2.465	**0.015**	-0.0046	1.103	0.270
MF	0.0023	0.959	0.339	0.0058	1.065	0.287	0.0037	0.529	0.597	-0.0021	0.273	0.785	-0.0045	1.284	0.199	0.0404	4.612	**< 0.001**	-0.0014	0.385	0.700
SF	0.0084	4.056	**< 0.001**	0.0035	0.631	0.528	0.0150	3.179	**0.002**	0.0068	1.566	0.117	0.0006	0.152	0.879	0.0350	3.871	**< 0.001**	0.0043	1.419	0.156
NE	0.0073	4.156	**< 0.001**	0.0009	0.162	0.872	0.0129	3.596	**< 0.001**	0.0170	2.843	**0.005**	-0.0046	1.354	0.176	0.0370	3.641	**< 0.001**	0.0029	1.103	0.270
SE	0.0066	3.446	**< 0.001**	0.0164	2.654	**0.008**	0.0032	0.782	0.4356	0.0000	0.001	0.992	-0.0018	0.466	0.641	0.0383	5.000	**< 0.001**	0.0072	2.445	**0.015**
G	0.0037	1.732	0.086	0.0198	2.088	**0.037**	0.0072	1.545	0.125	0.0016	0.581	0.562	-0.0127	1.187	0.235	0.0480	3.352	**0.001**	-0.0005	0.125	0.901

Table 2. The numbers of native species pooled over all plots within each habitat and each site separately. A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep; LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SF: south-facing edges, G: grasslands. Asterisks indicate cases where there were fewer than five plots per habitat.

Tabelle 2. Die aus allen Plots summierten Zahlen der heimischen Arten der einzelnen Habitate und Untersuchungsorte. A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep; LF: große Waldflächen, MF: mittelgroße Waldflächen, SF: kleine Waldflächen, NE: Waldränder mit nördlicher Ausrichtung, SF: Waldränder mit südlicher Ausrichtung, G: Grasland. Sterne markieren Habitate, an denen weniger als fünf Plots aufgenommen werden konnten.

	A	B	C	D	E
LF	37	33	38*	24*	32
MF	41	37	30	50	46
SF	42	54	70	63	74
NE	63	68	74	78	85
SE	49	55	70	67	76
G	40	41	42	40	58
Total	115	107	113*	115*	126

In the ordination scatterplot, DCA axis 2 (gradient length: 3.237) corresponded to the centre-to-periphery gradient (Fig. 3), which was associated with multiple environmental variables. Sites towards the centre of the basin proved to be associated with higher summer temperature and lower summer precipitation values than sites near the periphery of the basin. As for the soil factors, pH proved to be highly associated with the centre-to-periphery gradient, showing decreasing values towards the periphery. The proportion of contemporary anthropogenic habitat had the strongest influence on species composition in sites among all land-use factors. It showed an increasing trend towards the south (details on environmental factors are shown in Supplement E3).

4. Discussion

4.1 Trends in overall species richness

Our results showed an increase in species richness from the basin centre to the periphery for small forest patches, north-facing edges and south-facing edges. Although a similar trend seemed to prevail in the grassland habitat, it was not significant. Earlier studies suggested that increasing species richness should be expected with decreasing aridity in the grassland component of the forest-steppe (CHYTRÝ et al. 2007, KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2008), as a consequence of more favourable environmental conditions. The lack of a relationship for the grassland habitat in our study may be related to factors other than climate, such as site history (Supplement E1) or soil characteristics (Supplement E3).

As for the forest patches, CHYTRÝ et al. (2007) emphasized that their species richness should remain constant with increasing aridity, as a result of two processes: first, to a certain degree, the forest canopy is able to buffer the effects of increasing aridity; second, under more arid conditions, grassland species colonise forest interiors and offset the reduced number of mesic forest-related species. Our results suggest the validity of the first explanation: the richness of forest-related species remained approximately the same along the entire

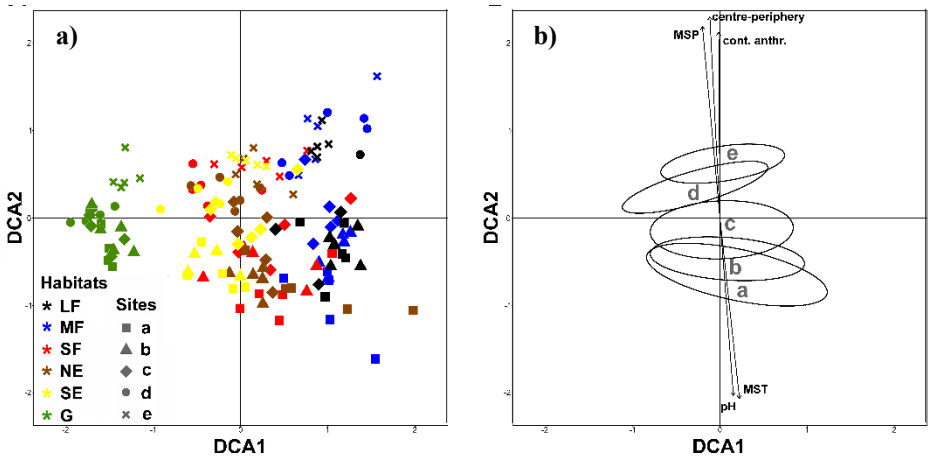


Fig. 3. a) DCA ordination scatterplot based on the presence-absence data of native species, using colours for habitats and symbols for sites. **b)** Biplot diagram of the same ordination. Ellipses around the sites were drawn using the standard deviations of the point scores. Only the variables with the highest correlations with ordination axes are displayed. The eigenvalues of the first and second axes are 0.421 and 0.258, respectively. MSP: mean summer precipitation, MST: mean summer temperature, cont. anthr: anthropogenic habitat cover in the contemporary map, centre-periphery: the latitudinal distance of the sites from the centre of the Carpathian Basin. Habitats: LF: large forest patches, MF: medium forest patches, SF: small forest patches, NE: north-facing edges, SE: south-facing edges, G: grasslands. Sites: A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep.

Abb. 3. a) DCA Ordinations-Streudiagramm basierend auf Präsenz-Absenz Daten der heimischen Arten, Farben kennzeichnen die unterschiedlichen Habitate, Symbole die Untersuchungsorte. **b)** Biplot-Diagramm der gelichen Ordination. Die Ellipsen um die Untersuchungsorte wurden mit den Werten für die Standardabweichungen der Punkt-Werte konstruiert. Nur die Umweltvariablen mit der größten Korrelation zu den Ordinationsachsen sind dargestellt. Die Eigenvalues der ersten und zweiten Achse betragen 0,421 bzw. 0,258. MSP: mittlerer Sommerniederschlag, MST: mittlere Sommertemperatur, cont. anthr.: Deckung anthropogen beeinflusster Habitate in aktueller Karte, centre-periphery: die latitudinale Distanz der untersuchten Untersuchungsorte vom Zentrum des Karpatenbeckens. Untersuchungsorte: A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep.

centre-to-periphery gradient in all studied habitats, despite the changes in aridity. In contrast, the second explanation does not seem likely, as forest or edge habitats showed no increase regarding the richness of either xeric grassland species ($S_{grassland}$) or sand grassland species (S_{sand}), suggesting that these species were not able to better colonise woody habitats with increasing aridity.

Dengler et al. (2014) pointed out that plot-scale richness peaks do not necessarily coincide with the peaks of the total species pool along climatic gradients, probably because different mechanisms govern species richness at different scales. However, plot-scale species richness and local species pools showed parallel trends in our study, which is similar to the findings of Kovács-Láng et al. (2000). This result suggests that two mechanisms operate simultaneously (Fekete et al. 2008): some species cannot reach the central parts of the Carpathian Basin (decreasing species pool), while others remain in the species pool, but their frequency gradually decreases (decreasing species richness per plot, i.e., lower species density).

4.2 Species richness trends across different phytosociological preference groups

We found an increase in the richness of xeric grassland species ($S_{grassland}$) towards the periphery in small forest patches and north-facing edges, but not in the other four habitats. Both KOVÁCS-LÁNG et al. (2000) and FEKETE et al. (2010) found that the number of xeric grassland species increased from the centre towards the periphery of the Danube-Tisza Interfluve. Similarly, we revealed an increasing species richness of sand grassland species (S_{sand}) towards the periphery for north-facing edges only, while none of the other habitats showed a similar trend. This trend is also in agreement with FEKETE et al. (2010) and KOVÁCS-LÁNG et al. (2000).

The lack of any significant centre-to-periphery trend for forest-related species (S_{forest}) in our study is in contrast with the results of KOVÁCS-LÁNG et al. (2000), who revealed an increasing richness towards the periphery. This contradiction could be explained by the regional topography and the direction of our gradient. It has been proposed that mountains served as propagule sources for forest species following the treeless vegetation period in the plains throughout the Middle Ages (FEKETE et al. 1999, 2010, BIRÓ et al. 2008). The study of KOVÁCS-LÁNG et al. (2000) encompassed a gradient from the centre to the northern/northwestern periphery. The latter is in close proximity to the foothills of the Carpathians and the Alps, which should have served as a source for forest species. Our study, by contrast, ranged from the centre to the south. Here, the distance to the next mountain range (Dinarides) is still high, and the forest species pool consequently small.

In our study, the richness of weeds (S_{weed}) showed a significant increase towards the periphery in all studied habitats, which was coupled with an increasing proportion of anthropogenic habitats, as indicated by the contemporary habitat map. Similarly, KOVÁCS-LÁNG et al. (2000) reported a slight increase in the richness of weed species towards the periphery. The higher level of anthropogenic disturbances may be considered a possible cause for the trend in the species richness of weeds. However, it is important to note that all weeds in our study were native and most of them natural constituents of intact or near-natural forest-steppe habitats (e.g., *Buglossoides arvensis*, *Cynoglossum officinale*, *Lamium amplexicaule*, *Viola arvensis*). Hence, the increase in the richness of weeds should not necessarily be interpreted as an indication of increased habitat degradation. Climatic and soil factors may at least partly be responsible for the observed pattern, although more studies are needed to provide us with a firm explanation.

The richness of adventives (S_{adv}) was conspicuously low at Site B (Bócsa). We believe this may be explained by the extremely low proportion of anthropogenic habitats, which were more common in all other sites. Anthropogenic habitats, including tree plantations, ploughlands, old-fields and abandoned farms, often serve as invasion hot-spots (PÁNDI et al. 2014, CSECSERITS et al. 2016).

4.3 Trends in species composition and environmental variables

It has been suggested that abrupt vegetation changes may prevail within the forest-steppe zone over very short latitudinal distances (e.g., WALTER & BRECKLE 1989, CHIBILYOV 2002, ZLOTIN 2002), although detailed studies have been relatively scarce. In line with the above suggestions, our results revealed marked changes in species composition over a distance of approximately 70 km. The existence of the forest-steppe zone is enabled by a subtle balance of numerous biotic and abiotic parameters, where several species and communities may be close to their distributional limits (WALTER & BRECKLE 1989, BORHIDI 2002). Even small

environmental shifts may result in considerable changes in vegetation (BARTHA et al. 2008), which is a likely explanation why we revealed strong changes in species composition across studied habitats, despite short geographic distances and moderate changes in the studied environmental variables.

Earlier studies explained that the observed centre-to-periphery trends with decreasing aridity were coupled with soil characteristics or land-use history (KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2008, 2011, FEKETE et al. 2010). Our study suggests the existence of a complex gradient, i.e. one consisting of several abiotic environmental factors operating simultaneously (WHITTAKER 1975). As shown by the DCA ordination, decisive environmental variables were highly correlated with the centre-to-periphery gradient (i.e., DCA axis 2). This finding calls for further research that disentangles the relevance of climatic, edaphic and land-use variables in order to gain a better understanding of the processes driving the observed phenomenon. It is important to keep in mind, however, that the studied environmental factors are not independent and might mask a more important unstudied variable, like water availability. For example, high sand fraction content could increase the effects of climatic aridity (VÁRALLYAI 1993). Additionally, the proportion of woody and non-woody habitats in a landscape may simultaneously reflect the effects of aridity and human activity.

4.4 Implications for conservation

According to MOLNÁR et al. (2012), forest-steppes of the Carpathian Basin belong to the most threatened vegetation types in the region. Additionally, European-scale simulations show that the Danube-Tisza Interfluve is extremely vulnerable to climate change (HICKLER et al. 2012). Space-for-time substitutions are considered valuable tools for predicting biotic responses to expected environmental changes (PICKETT 1989, BLOIS et al. 2013, ROLO et al. 2016, BÁTORI et al. 2017). The method has serious limitations and, therefore, it has to be applied with care. For example, it is clear from our study that there are multiple factors correlating with (and potentially underlying) the studied centre-to-periphery gradient. Nevertheless, as aridity plays a prominent role among the studied environmental factors, our gradient may be used to construct tentative predictions regarding vegetation responses to aridification (cf. MCLAUGHLIN et al. 2017). As emphasized by BARTHA et al. (2008), the centre-to-periphery aridity gradient in the Danube-Tisza Interfluve corresponds to environmental changes projected for the next few decades. In line with STEWART et al. (2010) and ČAVLOVIĆ et al. (2017), our study suggests that different habitat types and different phytosociological species groups may react differently to the aridity gradient. Thus, the negative effects of climate change may be mitigated by protecting the highest possible diversity of both habitats and phytosociological groups, as some of them will be less affected by increasing temperature and decreasing precipitation.

Erweiterte deutsche Zusammenfassung

Einleitung – Waldsteppen zählen zu den komplexesten Ökosystemen der nördlichen gemäßigten Zone. Die Biodiversität der Waldsteppen ist bemerkenswert, mit vielen endemischen und Rote-Liste Arten, sowie Arten mit besonderer Bedeutung im Naturschutz (ERDŐS et al. 2018a). Gleichzeitig gehören Waldsteppen zu den am stärksten bedrohten Biomen der Erde (HOEKSTRA et al. 2005). Die westlichsten Ausläufer der eurasatischen Waldsteppenzone befinden sich im Karpatenbecken (MAGYARI et al. 2010). Das Karpatenbecken weist eine zirkulare Zonalität auf: während die äußersten Gebiete des Beckens von Laubwäldern bedeckt sind, ist der mittlere Teil durch Waldsteppen charakterisiert (ob Steppe im Beckenzentrum eine natürliche Vegetation ist, ist aber umstritten) (FEKETE et al. 2014).

Schon in früheren Studien wurden Vegetationsgradienten vom Zentrum zur Peripherie analysiert. KOVÁCS-LÁNG et al. (2000) und BARTHA et al. (2011) haben gezeigt, dass der Artenreichtum im Grasland (sowohl die Artenzahl je Aufnahmefläche als auch der lokale Artenpool) zur Peripherie hin zunimmt. Da aber bewaldete Lebensraumtypen unberücksichtigt blieben, ist nicht bekannt, ob ein ähnlicher Gradient auch bei Waldinnenräumen und Waldrändern zu beobachten ist. Die Umweltfaktoren, die den Vegetationsgradienten verursachen, sind nicht vollständig erforscht: vermutlich spielt Aridität eine bedeutende Rolle, aber Boden, Landnutzung, und die geographische Entfernung von den hügeligen bzw. bergigen Regionen könnten auch wichtige Faktoren sein (KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2008, 2011, FEKETE et al. 2010). Ziel dieser Studie war es, die Zentrum-zu-Peripherie-Gradienten in verschiedenen Lebensräumen zu charakterisieren, und die effektiven Umweltfaktoren zu untersuchen. Von besonderem Interesse waren für uns folgende Fragen: (1) Wie ändern sich die Gesamtartenzahlen und die Artenzahlen der pflanzensoziologischen Gruppen entlang des Gradienten? (2) Wie ändern sich die Zusammensetzung der Arten und ausgewählte Umweltvariablen entlang des Gradienten?

Material und Methoden – Die folgenden fünf Untersuchungsorte wurden ausgewählt (vom zentralen bis zum südlichen Teil des Donau-Theiß-Zwischenstromlandes): Fülöpháza (Untersuchungsort A, N 46°52', E 19°25'), Bócsa (Untersuchungsort B, N 46°41', E 19°27'), Pirtó (Untersuchungsort C, N 46°28', E 19°26'), Kéleshalom (Untersuchungsort D, N 46°23', E 19°20'), und Négyestelep (Untersuchungsort E, N 46°17', E 19°35'). Die Jahresmitteltemperatur beträgt etwa 10,8 °C und der Jahresniederschlag liegt zwischen 530 und 570 mm (DÖVÉNYI 2010). Die natürliche Vegetation der Untersuchungsorte stellt ein Mosaik aus Wacholder-Pappelwald (*Junipero-Populetum albae* (Zólyomi ex Soó 1950) Szofridt 1969) und offenem Grasland (*Festucetum vaginatae* Rapaics ex Soó 1929 em. Borhidi 1996) dar. Wie schon in einer früheren Untersuchung eines ähnlichen Waldsteppen-Mosaiks (ERDŐS et al. 2015), haben wir sechs Lebensraumtypen unterschieden: große Waldflächen (> 0,5 ha), mittelgroße Waldflächen (0,2–0,4 ha), kleine Waldflächen (< 0,1 ha), Waldränder mit nördlicher Ausrichtung, Waldränder mit südlicher Ausrichtung und offenes Grasland. Insgesamt wurden 144 Vegetationsaufnahmen (25 m^2) im April und Juli 2016 nach der Methode von BRAUN-BLANQUET (1964) gemacht.

Unter den möglichen Prädiktoren für die Artenzahlen-Gradienten wurden folgende Faktoren analysiert: mittlerer Sommerniederschlag, mittlere Sommertemperatur (CarpatClim Database), Sand-Anteil im Boden, $CaCO_3$-Gehalt, pH-Wert, Humusgehalt, Wassergehalt und Feldkapazität (aus der digitalen Bodenkarte der DOSoReMI.hu initiative), Landnutzungsgeschichte des 18. Jahrhunderts (BIRÓ 2003, basierend auf der 1. Militärischen Übersicht, HM HIM), Landnutzungsgeschichte des 19. Jahrhunderts (basierend auf der 2. militärischen Übersicht, HM HIM 2005) und aktuelle Landnutzung (nach BIRÓ et al. 2006).

Für jede Aufnahme wurde der Artenreichtum an einheimischen (S_{nat}) und adventiven (S_{adv}) Arten berechnet. Einheimische Arten wurden gemäß ihren pflanzensoziologischen Präferenzen den folgenden pflanzensoziologischen Gruppen (BORHIDI 1995) zugeordnet: (1) Arten von Trockenrasen (*Festuco-Brometea*, *Festucetalia valesiacae*, *Festucion valesiacae*, *Sedo-Scleranthetea*, *Sedo-Scleranthetalia*, *Alysso-Sedion*, *Corynephoretalia*, *Festuco-Sedetalia*), (2) Arten von offenen Sandrasen (*Festucetalia vaginatae*, *Festucion vaginatae*, *Bromion tectorum*), (3) Arten von Wäldern, Waldrändern und Gebüschen (*Querco-Fagetea*, *Quercetea pubescentis-petraeae*, *Aceri tatarico-Quercion*, *Prunetalia spinosae*, *Trifolio-Geranietea*, *Geranion sanguinei*), (4) Arten von Unkrautgesellschaften (*Chenopodietea*, *Polygono-Chenopodietalia*, *Secalietea*, *Secalietalia*, *Arction lappae*, *Calystegietalia*, *Glechometalia*, *Onopordion acanthii*, *Dauco-Melilotion*), (5) indifferente Arten und (6) andere Arten (*Molinio-Arrhenatheretea*, *Molinietalia*, *Artemisio-Festucetalia*). Für alle Aufnahmen wurde die Anzahl der Arten in den Gruppen 1–5 berechnet ($S_{grassland}$, S_{sand}, S_{forest}, S_{weed}, S_{indiff}). Wegen der sehr geringen Artenzahl wurde Gruppe 6 nicht analysiert.

Wir definierten den Zentrum-zu-Peripherie-Gradienten mit der latitudinalen Distanz der untersuchten Untersuchungsorte vom zentral im Karpatenbecken lokalisierten Untersuchungsort Fülöpháza. Wir nutzten Poisson generalisierte lineare Modelle (GLMs) mit Lebensraumtyp als kategorisch erklärender und die latitudinale Distanz als kontinuierlicher erklärender Variable. Wir prüften auf einen linearen

Zusammenhang zwischen latitudinaler Distanz der einzelnen Untersuchungsorte und den Artenzahlen der unterschiedenen Artengruppen. Die statistischen Untersuchungen wurden mit R (version 3.4.3, R CORE TEAM 2017) unter Anwendung des lm4-Pakets (BATES et al. 2015) durchgeführt. Wir errechneten auch die Gesamtanzahl einheimischer Arten in jedem Habitat der einzelnen Untersuchungsorte indem wir die Daten aller Aufnahmeflächen der entsprechenden Habitate summiert haben. Die Ähnlichkeiten in der Artenzusmmensetzung der Aufnahmeflächen sowie die Faktoren, welche die Änderungen beeinflussten, wurden mit einer detrended correspondence analysis (DCA) dargestellt, unter Verwendung von Präsenz-Absenz -Daten der einheimischen Arten. 20 Umweltvariablen (Anhang E1) und die latitudinale Distanz der untersuchten Untersuchungsorte vom zentral im Karpatenbecken wurden in den mit den Präsenz-Absenz -Daten der einzelnen Plots kalkulierten Raum projiziert und geprüft, welche Variablen den Gradienten am besten erklären.

Ergebnisse – In den 144 Aufnahmen konnten 219 Arten unterschieden werden, von denen 198 einheimisch und 21 adventiv waren. Der Artenreichtum der einheimischen Arten (S_{nat}) nahm von der Mitte zur Peripherie in kleinen Waldflächen, nach Norden gerichteten Waldrändern und nach Süden gerichteten Waldrändern signifikant zu. Der Artenreichtum der Adventiven Arten (S_{adv}) nahm in großen Waldflächen, nach Süden gerichteten Waldrändern und im Grasland in Richtung der Peripherie signifikant zu. Es gab einen signifikanten Anstieg im Reichtum von Trockenrasenarten ($S_{grassland}$) von der Mitte zur Peripherie in kleinen Waldflächen und nach Norden gerichteten Waldrändern. Der Artenreichtum der Sandrasenarten (S_{sand}) zeigte einen signifikant zunehmenden Trend von der Mitte zur Peripherie in den nach Norden gerichteten Waldrändern. In keinem der untersuchten Lebensräume gab es einen signifikanten Trend im Reichtum der Arten von Wäldern, Waldrändern und Gebüsche. Die Anzahl der Ruderalarten nahm von der Mitte zur Peripherie in allen untersuchten Lebensräumen signifikant zu. Der Artenreichtum der indifferenten Arten (S_{indiff}) nahm von der Mitte zur Peripherie in den nach Süden gerichteten Waldrändern zu. Für die meisten Habitate fanden wir eine offensichtliche Zunahme bei den aufsummierten Arten entlang des Zentrum-zur Peripherie Gradienten. Die DCA zeigte auf der Achse 1 eine Sortierung der Plots nach den Habitat-Typen, während die Achse 2 mit den Zentrum-zu-Peripherie Gradienten anzeigte. Untersuchungsorte in der Nähe des Zentrums des Karpatenbeckens hatten höhere Sommertemperaturen und niedrigere Sommerniederschlagswerte als die Untersuchungsorte an der Peripherie.

Unter den Bodenfaktoren war pH-Wert eng mit dem Zentrum-zu-Peripherie Gradienten verknüpft: seine Werte nahmen entlang des Gradienten ab. Bezüglich der Landnutzungsfaktoren zeigten die aktuellen Daten den stärksten Einfluss auf die Artenzusammensetzung der Flächen.

Diskussion – Unsere Ergebnisse zeigten eine Zunahme des Artenreichtums in den kleinen Waldflächen, in den Waldrändern mit nördlicher Ausrichtung, sowie in den Waldrändern mit südlicher Ausrichtung. Obwohl ein ähnlicher Trend für das Grasland zu existieren schien, war dies nicht signifikant. Ältere Arbeiten vermuteten eine Zunahme der Artenzahlen mit abnehmender Aridität im Grasland-Kompartiment der Waldsteppe (CHYTRÝ et al. 2007, KOVÁCS-LÁNG et al. 2000, BARTHA et al. 2008). Hinsichtlich des Wald-Kompartimentes haben CHYTRÝ et al. (2007) jedoch gezeigt, dass die Artenzahlen mit zunehmender Aridität konstant bleiben kann, und zwar als Ergebnis zweier Prozesse: erstens kann die Baumkronenschichte die Effekte zunehmender Aridität bis zu einem gewissen Ausmaß abpuffern und zweitens können bei zunehmender Aridität Arten der Trockenrasen in die Wälder einwandern und so den Verlust von Waldarten mit höheren Feuchtigkeitsansprüchen ausgleichen. Unsere Ergebnisse können die erste Annahme bestätigen: die Artenzahlen der Waldarten änderten sich entlang des Zentrum-zur-Peripherie-Gradienten, trotz der Ariditätsunterschiede, kaum. Jedoch können unsere Ergebnisse die zweite Annahme nicht bestätigen: Wälder und Waldränder zeigten keine Artenzunahme entlang des Gradienten, weder was die Arten des trockenen Graslandes ($S_{grassland}$) angeht noch die Arten des Sandgraslands (S_{sand}), d. h. in unserer Studie waren trockenheitsertragende Graslandarten nicht in der Lage, Waldstandorte zu besiedeln.

Wir konnten nachweisen, dass Arten der Trockenrasen in Richtung Peripherie zwar in den kleinen Waldinseln und an den Nordseiten der Waldinseln zunahmen, nicht jedoch in den anderen vier Habitaten. Sowohl KOVÁCS-LÁNG et al. (2000) als auch FEKETE et al. (2010) stellten eine Zunahme von

Arten des Trockengraslandes vom Zentrum in Richtung Peripherie im Donau-Theiß-Zwischenstromland fest. Wir konnten eine Zunahme von Sandgraslandarten in Richtung Peripherie ausschließlich an Nordrändern der Waldinseln nachweisen, während die anderen Habitate keinen solchen Trend zeigten. Dies stimmt gut mit den Erkenntnissen von FEKETE et al. (2010) und KOVÁCS-LÁNG et al. (2000) überein.

Das völlige Fehlen eines signifikanten Zentrum-zur-Peripherie-Gradienten für Waldarten (S_{forest}) in unserer Studie steht im Widerspruch zu den Ergebnissen von KOVÁCS-LÁNG et al. (2000), die eine Artenzunahme in Richtung Peripherie nachweisen konnten.

In unserer Arbeit zeigten die Ackerbeikräuter (S_{weed}) zur Peripherie hin einen bemerkenswerten Anstieg der Artenzahlen für alle untersuchten Habitate. Dies steht in Zusammenhang mit der Zunahme von anthropogen überprägten Standorten, wie auch die aktuelle Biotopkarte zeigt. Ähnliches haben auch KOVÁCS-LÁNG et al. (2000) beobachtet. Der Zahl von adventiven Arten (S_{adv}) waren auffällig niedrig am Untersuchungsort B (Bócsa). Wir gehen davon aus, dass dies hier mit dem sehr geringen Anteil an anthropogen überprägten Habitaten erklärt werden kann, welche in den anderen Untersuchungsgebieten viel höhere Anteile zeigten.

Abrupte Veränderungen können innerhalb der Waldsteppenzone vorkommen, sogar über sehr kurze Entfernungen (WALTER & BRECKLE 1989, CHIBILYOV 2002, ZLOTIN 2002). Die Waldsteppen-Zone verdankt ihre Existenz einem nuancierten Gleichgewicht zwischen zahlreichen biotischen und abiotischen Faktoren, wobei mehrere Arten und Pflanzengesellschaften nahe ihren Verbreitungsgrenzen sind (WALTER & BRECKLE 1989, BORHIDI 2002). Es kann vermutet werden, dass in der Nähe von Verbreitungsgrenzen selbst geringe Umweltveränderungen erhebliche Veränderungen der Vegetation hervorrufen können (BARTHA et al. 2008). Dies kann eine mögliche Erklärung dafür sein, dass wir trotz der kurzen Entfernung deutliche Unterschiede sowohl im Artenreichtum als auch in der Artenzusammensetzung gefunden haben.

Unsere Studie weist auf die Existenz eines komplexen Gradienten hin, insbesondere auf einen Gradienten der mehrere abiotischer Umweltfaktoren vereint, die gleichzeitig, aber unabhängig voneinander wirken (WHITTAKER 1975). Wie die DCA Analyse zeigt, sind die maßgeblichen Umweltfaktoren stark mit dem Zentrum-zur-Peripherie-Gradienten korreliert (also die DCA Achse 2).

Wie schon BARTHA et al. (2008) hervorhoben, entspricht der Zentrum-zu-Peripherie Aridităts-Gradient im Donau-Theiß-Zwischenstromland den für die nächsten Dekaden vorhergesagten Klimaveränderungen. Basierend auf unseren Ergebnissen kann ein signifikanter Rückgang der Gefäßpflanzenartenzahlen mit zunehmender Erderwärmung erwartet werden. Dabei muss beachtet werden, dass zwischen unterschiedlichen Habitaten und pflanzensoziologischen Artengruppen Unterschiede in der Reaktion auf Klimaänderungen bestehen.

Author contribution statement

LE and GyK-D conceived the idea and the study design. LE, ZB, MM, and CsT performed the field works, ÁB-F, MB, ND, LP, PhS, KSz, and CsT performed the computations, LE wrote the manuscript, and all authors critically revised the manuscript.

Acknowledgements

LE was supported by grant OTKA PD 116114, ÁBF and MB by grant GINOP-2.3.2-15-2016-00019, and ZB by grant NKFIH K 124796.

Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Habitat maps for the five study sites from the 18th and 19th centuries, and current habitat distribution.

Anhang E1. Habitatkarten der fünf Untersuchungsgebiete aus dem 18. Und 19. Jahrhundert und die aktuelle Habitatverbreitung.

Supplement E2. List of adventives species and phytocoenological species groups.

Anhang E2. Liste der Andventiven und der phytozönologischen Artengruppen.

Supplement E3. Mean predictor values across sites, and their goodness of fit (R^2) and significance (p) in the DCA ordination.

Anhang E3. Mittlere Prädiktor-Werte an den Untersuchungsorten, ihre goodness of fit (R^2) und Signifikanz (p) in der DCA Ordination.

Supplement E4. Pairwise Pearson correlation among predictor variables.

Anhang E4. Paarweise Pearson-Korrelation zwischen den Prädiktorvariablen.

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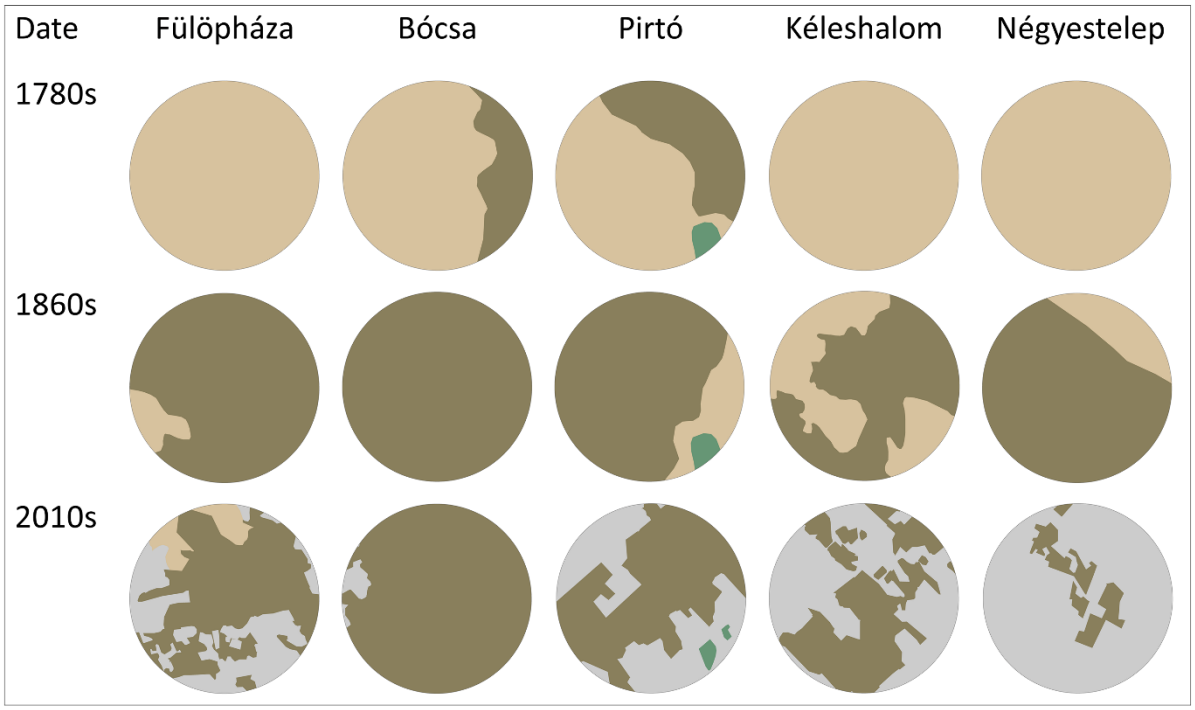
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Supplement E1. Habitat maps for the five study sites from the 18th and 19th centuries, and current habitat distribution. Dark brown: natural mosaic, light brown: dry sand grassland, green: other grassland, grey: anthropogenic habitat.

Anhang E1. Habitatkarten der fünf Untersuchungsgebiete aus dem 18. Und 19. Jahrhundert und die aktuelle Habitatverbreitung. Dunkelbraun: natürliches Mosaik, hellbraun: Sandtrockenrasen, grün: andere Grünlandtypen, grau: anthropogen überprägte Habitate.



Supplement E2. List of adventives species and phytocoenological species groups.

Anhang E2. Liste der Andventiven und der phytozönologischen Artengruppen.

Adventive species
Ailanthus altissima
Ambrosia artemisiifolia
Amorpha fruticosa
Armeniaca vulgaris
Asclepias syriaca
Cannabis sativa
Celtis occidentalis
Conyza canadensis
Elaeagnus angustifolia
Erigeron annuus
Gleditsia triacanthos
Juglans regia
Morus alba
Padus serotina
Pinus nigra
Pinus sylvestris
Populus nigra
Quercus cerris
Robinia pseudoacacia
Senecio vernalis
Tragus racemosus
Species of xeric grasslands
Achillea pannonica
Acinos arvensis
Allium oleraceum
Alyssum montanum
Anthemis ruthenica
Arabis recta
Artemisia campestris
Asparagus officinalis
Asperula cynanchica
Aster linosyris
Astragalus austriacus
Bothriochloa ischaemum
Bromus erectus
Bromus inermis
Carex humilis
Chamaecytisus ratisbonensis
Chrysopogon gryllus
Cruciata pedemontana
Dianthus pontederae
Elymus hispidus
Erigeron acris
Festuca rupicola
Festuca valesiaca
Helianthemum ovatum
Hieracium echioides
Linaria genistifolia
Linum austriacum
Linum hirsutum
Medicago minima
Melica transsilvanica
Minuartia glaucina
Minuartia glomerata
Muscari neglectum
Myosotis ramosissima
Myosotis stricta
Odontites lutea
Onosma arenaria

Phleum phleoides
Poa bulbosa
Potentilla arenaria
Pseudolysimachion spicatum
Saxifraga tridactylites
Scabiosa ochroleuca
Seseli annuum
Silene otites
Stipa borysthenica+capillata
Taraxacum laevigatum agg.
Tephroseris integrifolia
Teucrium chamaedrys
Thesium ramosum
Thymus pannonicus
Tragopogon dubius
Trinia ramosissima
Verbascum lychnitis
Veronica austriaca
Veronica praecox
Veronica prostrata

Species of open sandy grasslands

Achillea ochroleuca
Alkanna tinctoria
Alyssum tortuosum
Astragalus dasyanthus+exscapus
Bromus squarrosus
Carex liparicarpos
Centaurea arenaria
Colchicum arenarium
Dianthus serotinus
Echinops ruthenicus
Ephedra distachya
Equisetum ramosissimum
Euphorbia seguieriana
Festuca vaginata
Fumana procumbens
Gypsophila arenaria
Iris arenaria
Kochia laniflora
Koeleria glauca
Polygonum arenarium
Rhinanthus serotinus
Salix rosmarinifolia
Scirpoides holoschoenus
Secale sylvestre
Sedum urvillei
Silene conica
Syrenia cana
Tragopogon floccosus
Viola rupestris

Species of forests, edges, and scrubs

Berberis vulgaris
Carex flacca
Cephalanthera rubra
Clinopodium vulgare
Crataegus monogyna
Epipactis atrorubens
Euonymus europaeus
Fragaria viridis
Geranium sanguineum
Geum urbanum
Hylotelephium telephium
Ligustrum vulgare

Lithospermum officinale
Medicago falcata
Polygonatum latifolium
Polygonatum odoratum
Populus alba
Prunus spinosa
Quercus robur
Rhamnus catharticus
Rosa canina agg.
Ulmus minor
Viola hirta

Species of weed communities

Anthriscus cerefolium
Arabidopsis thaliana
Buglossoides arvensis
Camelina microcarpa
Chenopodium album
Consolida regalis
Cynoglossum officinale
Echium vulgare
Fumaria officinalis
Geranium columbinum
Geranium pusillum
Geranium robertianum
Lactuca serriola
Lamium amplexicaule
Lamium purpureum
Melilotus officinalis
Nepeta cataria
Saponaria officinalis
Setaria viridis
Sisymbrium orientale
Torilis arvensis
Veronica hederifolia
Vicia villosa
Viola arvensis

Indifferent species

Ajuga reptans
Alliaria petiolata
Anchusa officinalis
Arenaria serpyllifolia
Bromus arvensis
Bromus sterilis
Bromus tectorum
Calamagrostis epigeios
Capsella bursa-pastoris
Carex praecox
Carlina vulgaris
Cerastium semidecandrum
Chondrilla juncea
Cornus sanguinea
Crepis rhoeadifolia
Crepis tectorum
Cynodon dactylon
Dactylis glomerata
Daucus carota
Elymus repens
Erophila verna
Eryngium campestre
Euphorbia cyparissias
Falcaria vulgaris
Fallopia convolvulus
Galium aparine

Galium verum
Hieracium umbellatum
Holosteum umbellatum
Hypericum perforatum
Juniperus communis
Knautia arvensis
Leontodon hispidus
Luzula campestris
Medicago lupulina
Ononis spinosa
Ornithogalum umbellatum
Pimpinella saxifraga
Poa angustifolia
Poa compressa
Poa trivialis
Rubus caesius
Securigera varia
Silene alba
Solanum dulcamara
Solidago virgaurea
Stellaria media
Taraxacum officinale agg.
Thlaspi perfoliatum
Torilis japonica
Urtica dioica
Veronica arvensis
Veronica chamaedrys
Veronica triphyllos
Vicia angustifolia
Vincetoxicum hirundinaria
Other species
Acer sp.
Arrhenatherum elatius
Briza media
Carex stenophylla
Hieracium sp.
Molinia caerulea
Polygala comosa
Prunus sp.
Silene sp.

Supplement E3. Mean predictor values across sites (A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep), and their goodness of fit (R^2) and significance (p) in the DCA ordination.

Anhang E3. Mittlere Prädiktor-Werte an den Untersuchungsorten (A: Fülöpháza, B: Bócsa, C: Pirtó, D: Kéleshalom, E: Négyestelep), ihre goodness of fit (R^2) und Signifikanz (p) in der DCA Ordination.

	Sites						
	A	B	C	D	E	R^2	p
centre-to periphery gradient							
distance from the centre (km)	0	20.37	44.46	53.75	64.77	0.682	**< 0.001**
climatic parameters							
mean summer precipitation (mm)	178	180	185	189	187	0.621	**< 0.001**
mean summer temperature (°C)	20.62	20.58	20.50	20.44	20.49	0.553	**< 0.001**
soil parameters							
sand (m/m%)	94.70	91.92	92.47	82.46	90.55	0.290	**< 0.001**
$CaCO_3$ (m/m%)	7.09	6.62	4.07	5.88	6.19	0.036	0.054
pH	8.36	7.94	8.12	7.74	7.75	0.532	**< 0.001**
organic matter (m/m%)	1.39	1.37	1.59	1.52	1.33	0.011	0.426
water content at field capacity (V/V%)	12.39	13.40	13.85	19.07	11.69	0.056	**0.017**
18th-century habitat map							
natural mosaic (% cover)	0.00	20.85	33.93	0.00	0.00	0.119	**< 0.001**
dry sand grassland (% cover)	100.00	79.15	63.56	100.00	100.00	0.111	**< 0.001**
other grassland (% cover)	0.00	0.00	2.52	0.00	0.00	0.014	0.394
anthropogenic habitat (% cover)	0.00	0.00	0.00	0.00	0.00	0.000	1.000
19th-century habitat map							
natural mosaic (% cover)	93.07	100.00	82.62	60.32	84.84	0.298	**< 0.001**
dry sand grassland (% cover)	6.93	0.00	14.87	39.68	15.16	0.307	**< 0.001**
other grassland (% cover)	0.00	0.00	2.51	0.00	0.00	0.014	0.394
anthropogenic habitat (% cover)	0.00	0.00	0.00	0.00	0.00	0.000	1.000
contemporary habitat map							
natural mosaic (% cover)	59.21	97.30	58.10	44.56	11.07	0.518	**< 0.001**
dry sand grassland (% cover)	8.05	0.00	0.00	0.00	0.00	0.274	**< 0.001**
other grassland (% cover)	0.00	0.00	1.48	0.00	0.00	0.014	0.394
anthropogenic habitat (% cover)	32.74	2.70	40.42	55.44	88.93	0.580	**< 0.001**
protection							
years since protection	43	43	6	43	14	0.136	**< 0.001**

Supplement E4. Pairwise Pearson correlation among predictor variables. core-periphery: latitudinal distance from centre of the Carpathian Basin MSP: mean summer precipitation, MST: mean summer temperature, c.: century, cont.: contemporary, anthr.: anthropogenic.

Anhang E4. Paarweise Pearson-Korrelation zwischen den Prädiktorvariablen. core-periphery: die latitudinale Distanz der Untersuchungsorte vom Zentrum des Karpatenbeckens, MSP: mittlerer Sommerniederschlag, MST: mittlere Sommertemperatur, c.: Jahrhundert, cont.: aktuell, anthr.: anthropogen beeinflusst.

	core-periphery	MSP	MST	soil sand	soil $CaCO_3$	soil pH	soil organic matter	soil water content at field capacity	18^{th} c. natural mosaic	18^{th} c. dry sand grassland	18^{th} c. other grassland	19^{th} c. natural mosaic	19^{th} c. dry sand grassland	19^{th} c. other grassland	cont. natural mosaic	cont. dry sand grassland	cont. other grassland	cont. anthr.habitat	years since protection
core-periphery	1.000	**0.940**	**-0.918**	**-0.605**	**-0.510**	**-0.825**	0.210	0.292	-0.046	0.032	0.166	**-0.625**	**0.614**	0.166	**-0.686**	**-0.781**	0.166	**0.759**	**-0.575**
MSP	**0.940**	1.000	**-0.993**	**-0.806**	**-0.492**	**-0.797**	0.385	**0.578**	-0.150	0.133	0.122	**-0.852**	**0.844**	0.122	**-0.645**	**-0.690**	0.122	**0.709**	-0.375
MST	**-0.918**	**-0.993**	1.000	**0.831**	**0.538**	**0.792**	**-0.458**	**-0.641**	0.070	-0.054	-0.168	**0.861**	**-0.849**	-0.168	**0.552**	**0.732**	-0.168	**-0.622**	0.348
soil sand	**-0.605**	**-0.806**	**0.831**	1.000	0.121	**0.757**	-0.321	**-0.891**	0.342	-0.339	0.244	**0.882**	**-0.901**	0.244	0.284	**0.510**	0.244	-0.342	-0.232
soil $CaCO_3$	-0.510	**-0.492**	**0.538**	0.121	1.000	0.086	**-0.822**	-0.213	**-0.701**	**0.724**	**-0.919**	0.367	-0.299	**-0.919**	0.123	**0.542**	**-0.919**	-0.163	**0.756**
soil pH	**-0.825**	**-0.797**	**0.792**	**0.757**	0.086	1.000	0.094	**-0.423**	0.231	-0.238	0.294	**0.513**	**-0.536**	0.294	0.398	**0.804**	0.294	**-0.488**	0.084
soil organic matter	0.210	0.385	**-0.458**	-0.321	**-0.822**	0.094	1.000	**0.592**	**0.525**	**-0.548**	**0.762**	**-0.570**	**0.514**	**0.762**	0.094	-0.254	**0.762**	-0.080	-0.293
soil water content at field capacity	0.292	**0.578**	**-0.641**	**-0.891**	-0.213	**-0.423**	**0.592**	1.000	-0.120	0.116	-0.044	**-0.834**	**0.839**	-0.044	0.045	-0.324	-0.044	-0.006	0.365
18^{th} c. natural mosaic	-0.046	-0.150	0.070	0.342	**-0.701**	0.231	**0.525**	-0.120	1.000	**-0.999**	**0.818**	0.294	-0.356	**0.818**	**0.533**	-0.390	**0.818**	**-0.496**	**-0.463**
18^{th} c. dry sand grassland	0.032	0.133	-0.054	-0.339	**0.724**	-0.238	**-0.548**	0.116	**-0.999**	1.000	**-0.840**	-0.274	0.337	**-0.840**	**-0.508**	0.385	**-0.840**	**0.473**	**0.487**
18^{th} c. other grassland	0.166	0.122	-0.168	0.244	**-0.919**	0.294	**0.762**	-0.044	**0.818**	**-0.840**	1.000	-0.058	-0.017	**1.000**	0.073	-0.250	**1.000**	-0.064	**-0.727**
19^{th} c. natural mosaic	**-0.625**	**-0.852**	**0.861**	**0.882**	0.367	**0.513**	**-0.570**	**-0.834**	0.294	-0.274	-0.058	1.000	**-0.997**	-0.058	**0.495**	0.331	-0.058	**-0.522**	0.035
19^{th} c. dry sand grassland	**0.614**	**0.844**	**-0.849**	**-0.901**	-0.299	**-0.536**	**0.514**	**0.839**	-0.356	0.337	-0.017	**-0.997**	1.000	-0.017	**-0.501**	-0.313	-0.017	**0.528**	0.020
19^{th} c. other grassland	0.166	0.122	-0.168	0.244	**-0.919**	0.294	**0.762**	-0.044	**0.818**	**-0.840**	**1.000**	-0.058	-0.017	1.000	0.073	-0.250	**1.000**	-0.064	**-0.727**
cont. natural mosaic	**-0.686**	**-0.645**	**0.552**	0.284	0.123	0.398	0.094	0.045	**0.533**	**-0.508**	0.073	**0.495**	**-0.501**	0.073	1.000	0.093	0.073	**-0.994**	**0.483**
cont. dry sand grassland	**-0.781**	**-0.690**	**0.732**	**0.510**	**0.542**	**0.804**	-0.254	-0.324	-0.390	0.385	-0.250	0.331	-0.313	-0.250	0.093	1.000	-0.250	-0.200	**0.403**
cont. other grassland	0.166	0.122	-0.168	0.244	**-0.919**	0.294	**0.762**	-0.044	**0.818**	**-0.840**	**1.000**	-0.058	-0.017	**1.000**	0.073	-0.250	1.000	-0.064	**-0.727**
cont. anthr. habitat	**0.759**	**0.709**	**-0.622**	-0.342	-0.163	**-0.488**	-0.080	-0.006	**-0.496**	**0.473**	-0.064	**-0.522**	**0.528**	-0.064	**-0.994**	-0.200	-0.064	1.000	**-0.505**
years since protection	**-0.575**	-0.375	0.348	-0.232	**0.756**	0.084	-0.293	0.365	**-0.463**	**0.487**	**-0.727**	0.035	0.020	**-0.727**	**0.483**	**0.403**	-0.727	**-0.505**	1.000

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Zeitschrift/Journal: Tuexenia - Mitteilungen der Floristisch-soziologischen Arbeitsgemeinschaft

Jahr/Year: 2019

Band/Volume: NS_39

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Artikel/Article: Trends in species composition and richness along a centre-to-periphery gradient in forest-steppes of the southern Carpathian Basin Trends in Artenzusammensetzung und -reichtum von Waldsteppen entlang eines Zentrum-zur-Peripherie-Gradienten im südlichen Karpatenbecken 357-375