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Grassland vegetation in urban habitats – testing ecological theories

Graslandvegetation im urbanen Raum – Überprüfung einiger ökologischer Theorien

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Abstract

During the last millennium, urbanization has considerably changed natural ecosystems and formed new artificial habitats. Habitat loss and changes in the abiotic environment are seriously affecting urban biodiversity. We investigated the vegetation composition of three urban habitat types, vacant lots, urban parks, and peri-urban grasslands, which are characterised by species typical to semi-natural grasslands and ruderal assemblages in the city of Debrecen (East-Hungary). We used five spatial replicates of each habitat type and five random plots (5 m × 5 m) in every site for our analyses. We tested the following hypotheses: (1) lower species numbers and Shannon diversity, and a higher proportion of weeds and disturbance-tolerant species are present in the city centre (i.e. urban parks) compared to more peripheral habitats (vacant lots and peri-urban grasslands), (2) the proportion of warm- and nitrogen-demanding species increases, while the proportion of moisture-demanding species decreases in habitats typical to city centres (3) we also tested the increase in cosmopolitan and alien species and the decrease in species of the natural flora in habitats typical to city centres as predicted by the urban homogenisation hypothesis. We found that species composition of urban habitat types is considerably affected by the specific disturbances and site histories associated with the certain habitats. The most urbanised habitats, the urban parks harboured the lowest number of species and the lowest Shannon diversity. The ratio of weeds and disturbance-tolerants was the highest in the city centre likely due to the high-intensity trampling and soil disturbances. Plant species of city centre were more drought-tolerant compared to peri-urban grasslands, which is likely due to the increased level of drainage. The ratio of nitrogen-demanding species was lower in urban parks and peri-urban grasslands than in vacant lots, likely due to the high level of recent soil disturbance in this habitat type. The proportion of alien species was high both in vacant lots and peri-urban grasslands, even though their disturbance regimes differed considerably. The proportion of cosmopolitan species was significantly higher in urban parks compared to vacant lots and peri-urban grasslands. The large proportion of alien and cosmopolitan species together with the continuous human disturbance put native species at a competitive disadvantage, and accordingly the proportion of these species was lowest in the city centre. Even though the studied urban habitat patches did not contribute considerably to the preservation of rare or endangered plant species, they have an essential role in preserving the last remnants of grasslands in intensively used landscapes, and can be a good basis for urban greening projects.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Over the last millennium, urbanization has induced fundamental and irreversible changes in the landscape composition and ecosystem functioning worldwide by altering natural ecosystems and forming new artificial habitats (McKinney 2008, Magura et al. 2010, Lososová et al. 2011, Williams et al. 2015). Urbanisation affects biodiversity in many ways: it alters the abiotic environment (such as temperature, soil characteristics, water availability; Sukopp 2004, Kühn & Klotz 2006, Csorba & Szabó 2012) and leads to considerable loss and isolation of natural habitats (McKinney 2006, LaPaix & Freedman 2010). Urban ecosystems are characterised by a fine-scale pattern of various habitat types, which are usually heavily disturbed and enriched in nutrients (Lososová et al. 2012a). Several anthropogenic disturbance regimes are associated with urban habitats, such as trampling, soil disturbance and pollution (Kowarik 1995, Sukopp 2004, LaPaix & Freedman 2010, Simon et al. 2011, 2013, Vince et al. 2014). Several studies have reported that land use intensity and the level of disturbances decrease from city centres towards peri-urban areas (McDonnell & Hahs 2008, Magura et al. 2013). Species diversity of urban habitats is considerably influenced by the various disturbance levels, which affect both the magnitude of the inter- and intra-specific competition and the ratio of disturbance adapted species (Connell 1978, Magura et al. 2004). For instance Magura et al. (2004) found that in urban environments species richness decreases with the increasing levels of disturbance; which was verified by their studies on rove beetles in East-Hungarian urban habitats. Beside the abovementioned factors in urban habitats, horticultural activity can considerably modify the natural flora by intensive management (e.g. mowing, fertilising, removal of woody vegetation, preferring grasses and herbs instead of woody species), and also by increasing the proportion of alien species by planting alien ornamental species (McKinney 2006, Lososová et al. 2012a, b, Huwer & Wittig 2013).

Despite this, urban habitats still play an important role in biodiversity conservation in cities. In many cities, urban green spaces preserve the remnants of the semi-natural habitats such as grasslands or forests, and they also have an important role in preserving at least a part of the regional species pool of semi-natural habitats (LaPaix & Freedman 2010). Urban areas can contain suitable habitats for numerous native plant species (McKinney 2006). In larger cities the number of native species is relatively high; for example half of the native flora of Germany, Belgium and the Netherlands occurs in Berlin, Brussels and in Maastricht respectively (Müller 2010). Various urban habitats, such as parks, vacant lots, rooftops, road verges and peri-urban grasslands can preserve and maintain urban biodiversity. Their species composition depends on their environmental characteristics, spatio-temporal dynamics, management and size (LaPaix & Freedman 2010, Cervelli et al. 2013). Furthermore urban habitats provide important ecosystem services for society such as purification of air and water, temperature regulation and water storage (Williams et al. 2009, Cervelli et al. 2013). A better understanding of the effect of urbanisation on ecosystem functions can support the development of strategies for the preservation of natural ecosystems within urban areas and for mitigating detrimental environmental impacts on human populations (Magura et al. 2013, Williams et al. 2015).

Urban grasslands comprising either the remnants of semi-natural grasslands or, in a broader sense, urban parks, residential green areas, road verges, are integral parts of the urban green area (KLAUS 2013). The example of Berlin, where the 5% of urban habitats are grasslands (43% of them have been assigned to protected grassland types), demonstrates that urban grasslands can considerably contribute to biodiversity conservation and can compensate the loss of grassland habitats in peri-urban regions (FISCHER et al. 2003). Even though the situation in most cities is less optimal for grassland species compared to Berlin, urban grasslands still have a great potential for harbouring a high plant and animal diversity (KLAUS 2013). When assessing the biodiversity potential of urban grasslands it should be noted that the majority of them are novel ecosystems, driven by considerable current and past anthropogenic disturbances and by the specific urban biotic and abiotic conditions (HOBBS et al. 2006, LOSOSOVÁ et al. 2011). Generally, each urban habitat type can be characterised by a special combination of these factors (MCDONNELL & HAHS 2008). In their comparative study of 32 European cities, LOSOSOVÁ et al. (2011) studied the effects of climate and wide range of habitat types from historical city centres to early successional and mid-successional sites on the species composition of vascular plants. They found that variation in the species composition of vascular plants is mainly related to the differences between habitat types.

In our study we investigated the vegetation of three urban habitat types (vacant lots, urban parks, and peri-urban grasslands) characterised by species typical to semi-natural grasslands and ruderal assemblages. In particular we proposed the following hypotheses: (1) The intermediate disturbance hypothesis (IDH) assumes that diversity and disturbance have an unimodal relationship (CONNELL 1978); above a certain level of disturbance, in the declining slope of the unimodal curve, which is represented by our highly disturbed urban habitats, increasing level of disturbance results in a decreased diversity. Thus we expect lower species numbers and Shannon diversity in highly disturbed habitats of the city centres. As an indicator of disturbance we expect a higher proportion of weeds and disturbance-tolerant species in the more disturbed habitats. (2) Urban environmental conditions are among the main filters shaping the species pool of urban habitats (WILLIAMS et al. 2015). We expect an increase in the ratio of warm- and nitrogen-demanding species and a decrease in the ratio of moisture demanding species in habitats typical to city centres compared to the peri-urban grasslands. (3) According to the urban homogenisation hypothesis, urbanisation has a strong homogenisation effect on the species pool of the cities, making the vegetation in the cities across the globe more similar than would be otherwise expected (MCKINNEY 2006). The intensity of homogenisation shows a positive correlation with the level of disturbance; thus, urban core areas are more affected in this respect than peri-urban areas (KÜHN & KLOTZ 2006, LAPAIX & FREEDMAN 2010). We predict a larger proportion of cosmopolitan and alien species in the more disturbed habitats, resulting in a decrease in the proportion of species of the natural flora.

2. Material and Methods

2.1 Study area

The study area is in the city of Debrecen (eastern Hungary). Its mean elevation is 121 m a.s.l., the surface area of the city is 461 km^2, the number of inhabitants is 207,594 (HUNGARIAN CENTRAL STATISTICAL OFFICE 2015). The climate of the region is continental; mean annual temperature is around 10 °C, annual precipitation is 590 mm (MAROSI & SOMOGYI 1991). We investigated three typical open urban habitat types that have the potential to harbour spontaneous grassland flora in the studied city. These habitats were vacant lots, urban parks and peri-urban grasslands. These habitats have different site histories, current disturbance regimes and positions in the urban ecosystem of Debrecen. Vacant lots are unsealed surfaces in the city centre originating from the demolition of buildings (Fig. 1). They are in an early successional stage and persist only for a few years (maximum 10 years) before being built on again. They are characterised by a high level of trampling, as the local population generally use them for recreation or as parking places. They generally harbour weedy vegetation composed of herbaceous species and are mown once or twice a year following the local weed control regulations. Urban parks are several decades old permanent green spaces that provide recreational space for citizens. They are characterised by open vegetation, predominantly grassland and scattered woody vegetation. The most significant disturbance factor is high intensity trampling and frequent mowing. They have a highly disturbed, unstructured soil. These places are mown at least once during the vegetation period, but typically they are mown several times a year. Peri-urban grasslands are large, persistent habitats around the inbuilt areas of the city. They are oldfields or levelled abandoned industrial spaces in a mid-successional stage. Their typical age is between 10–30 years, and characterised by spontaneously recovering grassland. Mainly due to financial limitations, they are mown only once a year. While vacant lots and urban parks are isolated from semi-natural grasslands by urban surfaces that are hostile to plant life, the level of isolation is lower in case of peri-urban grasslands. Based on our experiences and information from the literature, we assumed that habitats of the city centres are characterised by a higher level of disturbance compared to the habitats located outside the heavily urbanised area. We studied the effects of the different disturbance levels indirectly by concentrating on the differences between the distinct habitat types.

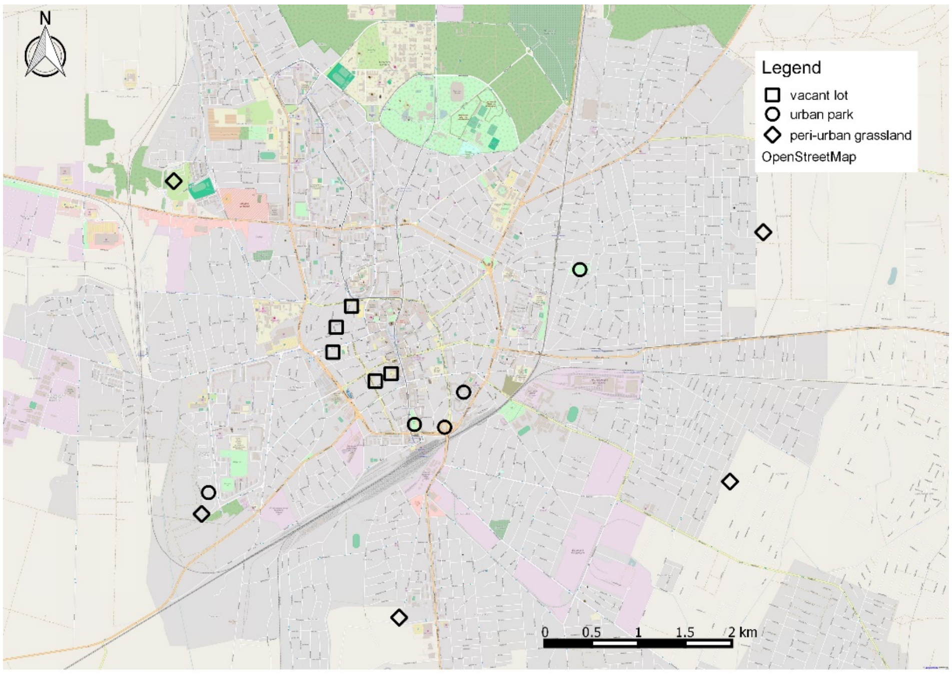

Fig. 1. Map of Debrecen with the position of the studied habitat patches. The urban area is indicated by a darker grey colour. Source of the map: © OpenStreetMap contributors.

Abb. 1. Karte von Debrecen mit der Lage der Untersuchungsflächen. Das Stadtgebiet ist dunkelgrau kenntlich gemacht. Quelle: © OpenStreetMap contributors.

2.2 Sampling design

Using the Urban Atlas (European Environmental Agency 2014) and aerial photographs we chose five representative sites of each of the three studied habitat types (vacant lots, urban parks, and peri-urban grasslands); altogether we studied 15 sites. We designated five random sampling plots of 5×5 metres in every site, thus we surveyed 25 plots in each habitat type and a total of 75 plots. The mean area of the sites was 2 667.4 m^2 ± 1 161.5 SE in vacant lots, 21 969.6 m^2 ± 8 248.9 SE in urban parks and 5 003.8 m^2 ± 1 446.5 SE in peri-urban grasslands. In the sampling plots we recorded the percentage cover of vascular plants in 2013. For the calculations we used only the records of natural and spontaneous vegetation including garden escapes and spontaneously established woody species, we excluded the planted species as we aimed to represent the natural responses of the vegetation.

2.3 Data analysis

We calculated species numbers and Shannon diversity for each plot, and we calculated total species numbers on the site level as a sum of species encountered in all plots. Species were assigned to four groups: alien species, weeds, disturbance-tolerant species and species of natural habitats using the categories of the social behaviour type general classification system (Borhidi 1995). As the social behaviour system contains 10 categories, we simplified it by aggregating groups of the main functional types. Adventive competitors (AC), invasives (I) and adventives (A) were considered as alien species. Ruderal competitors (RC) and weeds (W) were considered as weeds. Disturbance-tolerants (DT) and natural pioneers (NP) were considered as disturbance-tolerant species. Generalists (G), competitors (C) and specialists (S) were considered as species of natural habitats. We considered species as cosmopolitans based on the classification of Borhidi (1995). We calculated both relative species number and relative cover scores for social behaviour type groups and for cosmopolitan species for each plot. We used cover weighted scores of Ellenberg ecological indicator values for temperature, water, and nitrogen adapted to the Hungarian conditions (Borhidi 1995). We digitalised the borders of each site using ortho-photos provided by the open layers plug-in of the Quantum GIS 1.8 and calculated their area (Quantum GIS Development Team 2012).

We compared the vegetation characteristics of the habitat types using General Linear Models (GLM) and Tukey-tests (Zuur et al. 2009). As suggested by Sokal & Rohlf (1981) we used a nested design with habitat type, and sites were nested in habitat type as predictors and vegetation characteristics as dependent variables (total species number, Shannon diversity, relative species number and relative vegetation cover of the social behaviour types, ratio of the cosmopolitan species and cover weighted scores of Ellenberg ecological indicator values). For the calculations we used the plot data ($n = 75$). ANOVA and GLM analyses were calculated using Statistica 7.0 program. For comparing the vegetation of vacant lots, urban parks, and peri-urban grasslands we used Detrended Correspondence Analysis (DCA) based on specific cover scores. We used the cover weighted relative ecological indicators values TB (temperature), WB (moisture) and NB (nitrogen) as an overlay for the ordination (CANOCO 4.5; Lepš & Šmilauer 2003). The nomenclature follows Király et al. (2011) for taxa.

3. Results

We found altogether 140 species in the studied sites; there were 90 species in vacant lots, 44 in urban parks and 96 in peri-urban grasslands (Supplement E1–3). Total species numbers of the three habitat types differed significantly (ANOVA, $F = 7.68$, $p = 0.007$); urban parks harboured significantly fewer species compared to vacant lots and peri-urban grasslands (mean ± SE = 23.6 ± 1.47; 34.6 ± 2.50 and 34.4 ± 2.66 species/site, respectively). Species number and Shannon diversity of the plots were the lowest in urban parks and the highest in the peri-urban grasslands (Table 1). Both relative species number and relative cover scores of alien species were the highest in vacant lots and peri-urban grasslands and the lowest in

Table 1. Effect of habitat type and site on vegetation attributes (GLM and Tukey test; mean ± SE; $n = 75$). UP – urban parks, VL – vacant lots, PA – peri-urban grasslands. RS – relative species number, RC – relative vegetation cover. ***, $p < 0.001$; **, $p < 0.01$, *, $p < 0.05$, n.s., non-significant. Different letters in superscript indicate significant differences between the three habitat types (Tukey test).

Tabelle 1. Effekt des Habitattyps und Gebiets auf Vegetationsmerkmale (GLM und Tukey-Test; Mittelwerte ± SE; $n = 75$). UP – Stadtparks, VL – unbebaute Grundstücke, PA – Grasland am Stadtrand. RS – relative Artenzahl, RC – relative Deckung der Vegetation. ***, $p < 0{,}001$, **, $p < 0{,}01$, *, $p < 0{,}05$, n.s., nicht-signifikant. Unterschiedliche hochgestellte Buchstaben zeigen signifikante Unterschiede zwischen den drei Habitattypen (Tukey-Test).

	Mean ± SE			Effect of habitattype		Effect of site	
	UP	VL	PA	*F*	*p*	*F*	*p*
Total species number/plot	11.8 ± 0.5^a	14.6 ± 0.9^b	17.0 ± 0.8^c	20.57	***	4.82	***
Shannon diversity	1.6 ± 0.1^a	1.8 ± 0.1^b	2.2 ± 0.1^c	26.88	***	3.63	***
Social behaviour types							
RS of alien species	3.0 ± 1.0^a	10.3 ± 2.3^b	10.7 ± 1.7^b	11.65	***	6.06	***
RS of weeds	39.6 ± 2.5^a	43.0 ± 2.1^a	32.3 ± 1.9^b	9.86	***	4.40	***
RS of disturbance-tolerants	55.3 ± 3.0^a	43.4 ± 2.5^b	46.9 ± 1.9^b	9.61	***	4.63	***
RS of natural habitats	2.2 ± 0.7^a	3.4 ± 0.8^a	10.1 ± 1.2^b	30.47	***	4.02	***
RC of alien species	2.3 ± 1.6^a	$7.9 \pm 3.3a^b$	12.4 ± 3.6^b	5.04	**	5.52	***
RC of weeds	38.3 ± 4.9	34.3 ± 3.8	30.1 ± 2.5	2.04	n.s.	6.11	***
RC of disturbance-tolerants	57.6 ± 4.9^a	55.4 ± 3.3^{ab}	46.8 ± 3.7^b	4.37	*	7.96	***
RC of natural habitats	1.8 ± 1.2^a	2.5 ± 1.1^a	10.7 ± 2.4^b	10.9	***	2.39	*
Cosmopolitan species							
RS of cosmopolitan species	$57.6 + 2.0^a$	$32.0 + 2.7^b$	$27.5 + 1.8^b$	70.14	***	2.68	**
RC of cosmopolitan species	$69.2 + 4.1^a$	$33.0 + 4.5^b$	$25.6 + 2.4^b$	61.50	***	4.54	***
Ecological indicator values							
TB	5.6 ± 0.1	5.3 ± 0.1	5.3 ± 0.1	2.40	n.s.	0.96	n.s.
WB	4.3 ± 0.1^a	4.6 ± 0.1^{ab}	4.9 ± 0.2^b	5.42	**	4.24	***
NB	5.4 ± 0.2^a	6.0 ± 0.1^b	5.3 ± 0.2^a	6.67	*	3.36	***

urban parks. Weeds and disturbance-tolerant species were the most typical groups in each habitat types. The number of weed species was higher in vacant lots and urban parks compared to peri-urban grasslands, but we did not detect significant differences in cover scores. The number of disturbance-tolerant species was higher in vacant lots and peri-urban grasslands than in urban parks; however, their relative cover was the highest in urban parks. Both the relative number of species and cover of species typical for natural habitats were the highest in peri-urban grasslands. Both the relative species richness and relative cover of cosmopolitan species were the highest in urban parks. We detected no difference in the cover-weighted TB scores of the three studied zones. Cover-weighted WB scores were the highest in the peri-urban grasslands. Cover-weighted NB scores were the highest in vacant lots (Table 1).

In the DCA ordination, plots of the three habitat types were well separated (Fig. 2). Urban parks composed the most compact group which was characterised by *Carex hirta*, *Convolvulus arvensis*, *Cynodon dactylon*, *Geranium pusillum* and *Poa compressa*. Plots of va-

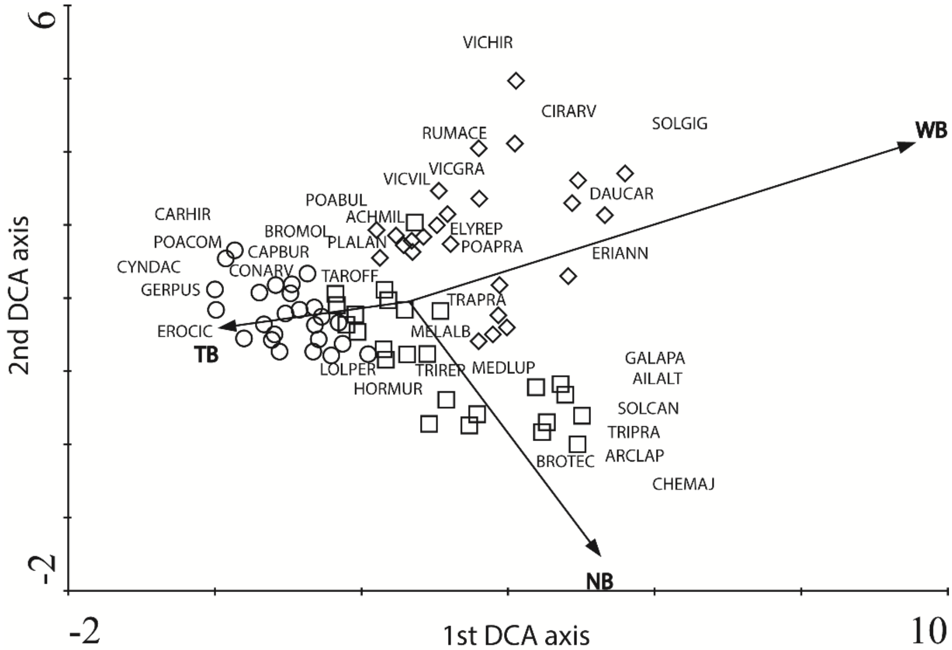

Fig. 2. DCA plot of the species composition of the studied habitats. Indicator values for temperature (TB), moisture (WB) and nitrogen (NB) scores were included as overlay. The first 35 species with highest cover scores are plotted. Circle – urban park; square – vacant lot; diamond – peri-urban grassland. Abbreviations of species names: ACHMIL – *Achillea millefolium*, ELYREP – *Elymus repens*, AILALT – *Ailanthus altissima*, ARCLAP – *Arctium lappa*, BROMOL – *Bromus mollis*, BROTEC – *Bromus tectorum*, CAPBUR – *Capsella bursa-pastoris*, CARHIR – *Carex hirta*, CHEMAJ – *Chelidonium majus*, CIRARV – *Cirsium arvense*, CONARV – *Convolvulus arvensis*, CYNDAC – *Cynodon dactylon*, DAUCAR – *Daucus carota*, EROCIC – *Erdodium cicutarium*, GALAPA – *Galium aparine*, GERPUS – *Geranium pusillum*, HORMUR – *Hordeum murinum*, LOLPER – *Lolium perenne*, MEDLUP – *Medicago lupulina*, MELALB – *Melandrium album*, PLALAN – *Plantago lanceolata*, POABUL – *Poa bulbosa*, POACOM – *Poa compressa*, POAPRA – *Poa pratensis*, RUMACE – *Rumex acetosella*, SOLCAN – *Solidago canadensis*, SOLGIG – *Solidago gigantea*, ERIANN – *Erigeron annuus*, TAROFF – *Taraxacum officinale*, TRAPRA – *Tragopogon pratensis*, TRIPRA – *Trifolium pratense*, TRIREP – *Trifolium repens*, VICGRA – *Vicia grandiflora*, VICHIR – *Vicia hirsuta*, VICVIL – *Vicia villosa*.

Abb. 2. DCA-Diagramm der Artenzusammensetzung des untersuchten Graslands. Zeigerwerte für Temperatur (TB), Feuchte (WB) und Stickstoff (NB) sind in das Diagramm eingeblendet. Die Position der 35 Arten mit der höchsten Deckung ist dargestellt. Kreise – Grasland in Stadtparks, Quadrate – Grasland auf unbebauten Grundstücken, Rauten – Grasland am Stadtrand. Für die vollständigen Artnamen siehe die englische Abbildungsunterschrift.

cant lots had a more heterogeneous pattern, typical species of this habitat were *Arctium lappa*, *Bromus tectorum*, *Chelidonium majus*, *Medicago lupulina*, *Trifolium pratense* and *T. repens*. Two alien invasive species *Ailanthus altissima* and *Solidago canadensis* were plotted here as well. *Taraxacum officinale* and *Lolium perenne* were typical both for urban parks and the vacant lots. Plots of peri-urban grasslands were scattered and characterised by species mainly typical for oldfields such as *Achillea collina*, *Cirsium arvense*, *Daucus carota*, *Plantago laceolata*, *Poa pratensis*, *Rumex acetosella*, *Vicia grandiflora* and *V. villosa*.

Typical alien species of this group were *Solidago gigantea* and *Erigeron annuus*. High cover-weighted WB values were typical for peri-urban grasslands and high cover-weighted NB values for the vacant lots.

4. Discussion

4.1 Effect of disturbance intensity

The findings supported our hypothesis; we found that the urban parks characterised by a high level of urbanisation and disturbance harboured the lowest number of species and the lowest Shannon diversity. Mid-successional peri-urban grasslands characterised by a low disturbance regime were the most species-rich among the studied habitat types. This is in line with the findings of other studies where they found that intensively managed recreational sites had the lowest species numbers compared to any other habitat types (SUKOPP 2004, LAPAIX & FREEDMAN 2010). In their study, LOSOSOVÁ et al. (2011) also found that species richness increased from the city centres towards the less urbanised urban peripheries. Continuous high-intensity disturbance in city centres supports weeds and disturbance-tolerant species but suppresses species of natural habitats (WILLIAMS et al. 2015). We detected a high proportion of weed species in all habitat types, however their cover scores were the highest in habitats of the city centre (vacant lots and urban parks). This was due to the frequent and intensive human disturbance such as trampling and soil disturbance which allows the establishment of these species (CERVELLI et al. 2013). Weed species can establish in these sites also by their enhanced dispersal (e.g. wind dispersal) or can germinate from their persistent seed bank (LOSOSOVÁ et al. 2011). Based on the results of the GLM it should be noted that vegetation of the sites showed a high level of variance, thus even though the observed trends are valid, the proportion of certain vegetation functional groups can vary due to the specific local conditions that we could not partial out in our model.

There was a marked difference in the species composition of the habitats; the species composition of urban parks, and the early- (vacant lots) and mid-successional (peri-urban grasslands) were well separated (see also the results of LOSOSOVÁ et al. 2011; Fig. 2). Urban parks and vacant lots were characterised by species typical to disturbed and ruderal habitats in an early successional stage, such as *Erodium cicutarium*, *Hordeum murinum*, *Melandrium album* and *Taraxacum officinale*. Moreover, we detected ruderal species such as *Convolvulus arvensis* and *Cynodon dactylon* which are highly resistant for trampling. High ratio of trampling-tolerant species is typical in urban habitats in Europe (LOSOSOVÁ et al. 2011, LUNDHOLM 2011).

We detected a considerable differences in the species composition of peri-urban grasslands compared to the vacant lots and urban parks due to their different origin and landscape context. Peri-urban grasslands were mostly characterised by segetal weed species absent from urban habitats but typical for old-fields (*Cirsium arvense*, *Elymus repens*, *Lepidium ruderale*, *Papaver rhoeas* and *Vicia villosa*) which likely immigrated from the neighbouring arable fields and from the residual seed bank (CERVELLI et al. 2013, MÁJEKOVÁ & ZALIBEROVÁ 2014, VALKÓ et al. 2016a). In case of disturbance-tolerant species we found a similar pattern: several species typical for the adjacent semi-natural grasslands were present in peri-urban grasslands, such as *Achillea collina*, *Daucus carota* and *Plantago lanceolata*.

4.2 Changes in environmental factors

The so-called "urban heat island effect" assumes that urban habitats are characterised by a higher temperature compared to their environments, which is mainly due to the higher rate of artificial surfaces (KOWARIK 1995, MCKINNEY 2006, MCDONELL & HAHS 2008). However, we did not find differences between the cover-weighted TB scores of the studied habitat types. The cover-weighted WB scores were the lowest in the urban parks and highest in peri-urban grasslands. The latter comprised mainly the species of semi-dry and semi-humid habitats. This is in line with the findings of other studies, where they found that plant species of city centres are more drought-tolerant compared to peri-urban grasslands (GODEFROID & KOEDAM 2007, WILLIAMS et al. 2015). This can be explained by the lack of asphalt surfaces, drainage and soil levelling in peri-urban grasslands (DOLAN et al. 2011, WILLIAMS et al. 2015). Thus, surface water can be retained and species typical to habitats with moist or wet soils (such as *Carex vulpina*, *Calystegia sepium*, *Juncus* spp. and *Phalaris arundinacea*) can establish in smaller depressions of peri-urban grasslands. Furthermore, invasives typical for peri-urban grasslands (especially *Solidago canadensis* and *S. gigantea*) are confined to mesophilous habitats. Species preferring high soil fertility are typical in urban habitats (PYŠEK 1995). In our study, species with high nitrogen (NB) score were the most typical for the vacant lots; corroborating reports of high nitrogen deposit and low depletion in city centres (LOSOSOVÁ at al. 2006, WILLIAMS et al. 2015). However, it should be taken in consideration as well, that ruderal species favouring soil disturbances are generally characterised by high NB values, thus the effect of nitrogen influx and disturbance cannot be perfectly separated in this case.

4.3 Homogenisation

Several studies found that relative cover of alien species increased in city centres (OLDEN & POFF 2003, KÜHN & KLOTZ 2006, CERVELLI et al. 2013). LOSOSOVÁ et al. (2012a) proposed that increased levels of disturbance, nutrient flux and alien propagule pressure are the main drivers of plant invasions. In our study we found that the ratio of alien species in the spontaneous flora were high both in the early-successional vacant lots with a high disturbance level and mid-successional peri-urban grasslands, which represented the lowest disturbance regime. Urban parks harboured the fewest alien species. Even though most studies found that strongly disturbed habitats are the most prone to plant invasions (CHYTRÝ et al. 2008, LOSOSOVÁ et al. 2012a), in our case likely the key factor was the successional stage of habitats, not the level of disturbance. This is in line with the findings of ALBERT et al. (2014), who found that the ratio of alien species is higher in younger habitats. In vacant lots the co-occurrence of early-successional age, the high levels of disturbance and the vicinity of potential propagule sources was likely responsible for the high proportion of the alien species. In this habitat *Ailanthus altissima*, *Celtis occidentalis* and *Solidago canadensis* were the most typical alien species. These species could establish in the habitat patches with a disturbed surface, their existence was supported by the low competitive ability of other species present (KELEMEN et al. 2016). The propagules of *A. altissima* and *C. occidentalis* most likely originated from the neighbouring areas. In peri-urban grasslands beside *Solidago gigantea*, *Erigeron annuus* and *Medicago sativa* were present making up large proportions of the vegetation. The presence of *E. annuus*, which is a typical species of old-fields in the region (ALBERT et al. 2014), and *M. sativa* might be a result of former agricultural cultivation and spontaneous immigration from neighbouring agricultural areas and old-fields. The proportion of cosmopolitan species was high in all studied habitat types similar to urban habitats situated in other European cities (LOSOSOVÁ et al. 2012a). In contrast to the proportion of alien species, the proportion of cosmopolitan species was significantly higher in the most disturbed urban parks compared to the vacant lots and peri-urban grasslands. This is in line with the findings of LOSOSOVÁ et al. (2012b) who found that more disturbed habitats are more affected by biotic homogenisation. Cosmopolitan species were represented mainly by species such as *Capsella bursa-pastoris*, *Convolvulus arvensis*, *Erodium cicutarium* and *Poa compressa*, which are fast growing and short-lived and well adapted to disturbed habitats (SUKOPP 2004).

Several studies found that the high ratio of cosmopolitan and alien species together with the continuous human disturbance puts native species at a competitive disadvantage, suppressing species typical to natural habitats (SUKOPP 2004, MCKINNEY 2006, HUWER & WITTIG 2013, WILLIAMS et al. 2015). Our results confirmed this pattern; we found the lowest proportion of species typical for the natural habitats in vacant lots and urban parks. These results partly contradict the findings of LOSOSOVÁ et al. (2012a) who found that in spite of the low species richness of parks they harbour a small proportion of alien species. Even in our case, the ratio of alien species was low, likely because the high level of isolation did not allow the species of natural grasslands to persist or re-establish due to the depleted soil seed banks and limited dispersal ability of grassland species (NOVÁK & KONVIČKA 2006). Only some species such as *Agrostis stolonifera*, *Poa pratensis*, *Potentilla recta* and *Veronica prostrata* were present in a few sites with low cover. As was also found by LOSOSOVÁ et al. (2012a) the ratio of species typical to natural habitats were significantly higher in mid-successional peri-urban grasslands where the studied sites harboured several species typical for semi-natural dry and mesophilous grasslands, such as *Achillea collina*, *Agrostis stolonifera*, *Astragalus cicer*, *Poa pratensis* and *Potentilla recta*.

5. Conclusions

In our study we found that species composition of urban habitat types was considerably affected by the specific disturbances and site histories associated with the certain habitats (see also LOSOSOVÁ et al. 2012a). The studied habitats were affected by various disturbance factors such as trampling, soil disturbances and mowing, which resulted in lower species diversity and a higher proportion of weeds and disturbance-tolerant species. In addition, in urban habitats the dry and nutrient-rich environment proved to be an important driver of the vegetation composition. The special conditions in urban habitats led to a homogenisation of the vegetation. In the vacant lots and urban parks we observed a significantly higher proportion of cosmopolitan species and a considerably lower proportion of species typical for the natural habitats compared to peri-urban grasslands. Although the studied urban habitat patches did not contribute considerably to the preservation of rare or endangered plant species, they still play an important role in preserving last remnants of grasslands in an intensively used landscape, and providing essential ecosystem services for the society. Moreover, even the smallest fragment of grasslands may contribute to the support of diversity of macroinvertebrates as pointed out by HORVÁTH et al. (2009, 2015).

Our study reveals that in many cities there is an urgent need for a conceptual naturalizing plan for the urban habitats by introducing species typical for natural habitats and providing proper management for them. As KLAUS (2013) points out, grassland restoration projects in urban environments have a considerable advantage compared to ones in agricultural landscapes, namely that in urban ecosystems there is no interest in maximizing the yield and long-term management is more feasible. We suggest using perennial, disturbance tolerant, competitor species of the local flora which can cope with the special urban conditions in such projects. Preferably the seeds should be originated from a local provenance to conserve the regional gene pool (VALKÓ et al. 2016b).

Erweiterte deutsche Zusammenfassung

Einleitung – Die fortschreitende Urbanisierung hat in den letzten Jahrhunderten zum Verlust natürlicher Ökosysteme aber auch zur Schaffung von neuen urbanen Lebensräumen geführt (LOSOSOVÁ et al. 2011). Diese urbanen Lebensräume können eine wichtige Rolle bei der Erhaltung der biologischen Vielfalt spielen, z. B. wenn in den Städten halbnatürliches Grasland entstanden oder erhalten geblieben ist (LAPAIX & FREEDMAN 2010). Urbanes halbnatürliches Grasland in Parks, auf Grünflächen, in Wohngebieten oder am Straßenrand kann einen wichtigen Teil des urbanen Naturpotenzials bilden (KLAUS 2013). Wir untersuchten die Vegetation dreier urbaner Graslandlebensräume, die von typischen Arten des halbnatürlichen Graslands aber auch von Ruderalarten aufgebaut werden. Konkret untersuchten wir die folgenden Hypothesen: (1) Im Stadtzentrum ist der Artenreichtum und die Shannon-Diversität des Graslands niedriger und der Anteil ruderaler und störungstoleranter Arten höher als am Stadtrand. (2) Im Stadtzentrum ist der Anteil wärme- und stickstoffliebender Arten im Grasland höher und der Anteil feuchteliebender Arten niedriger als am Stadtrand. (3) Im Stadtzentrum sind im Grasland die Anteile an Kosmopoliten und nicht-einheimischen Arten höher und der Anteil an Arten (halb-)natürlicher Habitate niedriger als am Stadtrand.

Methoden – In 2013 untersuchten wir in der Stadt Debrecen (Ost-Ungarn; Abb. 1) die drei urbanen Lebensräume: unbebaute Grundstücke im Stadtzentrum, Stadtparks im Stadtzentrum und Grasland am Stadtrand. Alle drei Lebensräume können grundsätzlich Arten des halbnatürlichen Graslands beherbergen, unterscheiden sich jedoch in ihrer Entstehungsgeschichte und ihrem Störungsregime sowie in ihrer Entfernung zum Stadtzentrum. Pro Lebensraumtyp untersuchten wir fünf Flächen, insgesamt 15. Pro Fläche wurden auf fünf zufällig ausgewählten 5 m × 5 m-Aufnahmeflächen (insgesamt 75) die Präsenz und Prozentdeckung aller Gefäßpflanzenarten erfasst. Bei der Auswertung wurden nur natürlich und spontan wachsende Arten (keine gepflanzten Arten) berücksichtigt. Die Arten wurden nach BORHIDI (1995) den Kategorien „Arten (halb-)natürlicher Habitate“, „nicht-einheimisch“, „kosmopolitisch“, „ruderal“ und „störungstolerant“ zugeordnet. Pro Aufnahmefläche wurden der Anteil dieser Artengruppen an der Gesamtartenzahl und der Anteil der Deckung der Artengruppen an der Gesamtdeckung berechnet. Zusätzlich wurden mit der Deckung gewichtete Zeigerwerte für Temperatur, Feuchte und Stickstoff berechnet (BORHIDI 1995). Wir nutzten zur Analyse General Linear Models (GLM) und Tukey-Tests mit dem Lebensraumtyp und der Fläche (eingeschachtelt in den Lebensraumtyp) als unabhängige Variablen und den Eigenschaften der Vegetation als abhängige Variablen. Zusätzlich wurde eine DCA-Ordination durchgeführt.

Ergebnisse – Der Artenreichtum und die Shannon-Diversität des Graslands waren in den Parks (im Stadtzentrum) am niedrigsten und im Grasland am Stadtrand am höchsten (Tab. 1). Der Artenreichtum und die Deckung der nicht-einheimischen Arten war auf unbebauten Grundstücken im Stadtzentrum und im Grasland am Stadtrand am höchsten. Ruderalarten und störungstolerante Arten waren typisch für alle drei Lebensräume. Die Anzahl der Ruderalarten war auf den unbebauten Grundstücken und in den Stadtparks höher als am Stadtrand. Der Artenreichtum störungstoleranter Arten war auf den unbebauten Grundstücken und am Stadtrand am höchsten, die Deckung der störungstoleranten Arten war jedoch in den Stadtparks am höchsten. Der Artenreichtum und die Deckung der Arten (halb-)natürlicher Standorte war am Stadtrand am höchsten. Die höchsten gewichteten Zeigerwerte für Feuchte wurden für das Grasland am Stadtrand berechnet; die gewichteten Zeigerwerte für Nährstoff waren auf den unbebauten Grundstücken am höchsten. In der DCA-Ordination waren die Aufnahmen der drei Graslandtypen klar voneinander getrennt, wobei die Stadtparks im Ordinationsdiagramm die kompakteste Gruppe mit geringsten floristischen Variabilität bildeten (Abb. 2).

Diskussion – Unsere Ergebnisse entsprechen der Hypothese, dass der am stärksten urbanisierte Lebensraum mit der stärksten Störung – die Stadtparks – am wenigsten Arten beherbergen und dementsprechend die niedrigste Shannon-Diversität besitzen. Andere Studien haben ebenfalls gezeigt, dass intensiv gepflegte Grünflächen am artenärmsten sind (SUKOPP 2004, LAPAIX & FREEDMAN 2010). Kontinuierliche Störungen von hoher Intensität im Stadtzentrum fördern störungstolerante Arten und unterdrücken Arten natürlicher Habitate (WILLIAMS et al. 2015). Charakteristisch für Stadtparks und unbebaute Grundstücke waren in unserer Studie Arten früher Sukzessionsstadien sowie ausdauernde Ruderalarten. Für das Grasland am Stadtrand waren hingegen Arten der Segetalflora charakteristisch, die im Stadtzentrum fehlten, jedoch typisch für Brachflächen sind. Wir konnten zeigen, dass im Stadtzentrum trockenheitstolerantere Arten als am Stadtrand vorkommen (WILLIAMS et al. 2015), was vermutlich auf den hohen Anteil versiegelter Flächen im Stadtzentrum und eine dadurch erhöhte Wasserabführung und auch Bodennivellierung zurückzuführen ist (DOLAN et al. 2011). Unbebaute Grundstücke waren durch Nährstoffzeiger charakterisiert – vermutlich aufgrund erhöhter Einträge von Stickstoff im Stadtzentrum (LOSOSOVÁ et al. 2006) sowie aufgrund von Störungen des Bodens in jüngerer Zeit. Der Anteil nicht-einheimischer Arten war sowohl im Grasland der unbebauten Grundstücke (als Folge der hohen Störungsintensität und des frühen Sukzessionsstadiums) als auch im Grasland am Stadtrand (gekennzeichnet durch geringe Störungsintensität und mittleres Sukzessionsstadium) hoch. Der Anteil der Kosmopoliten war in den Stadtparks am höchsten, wo auch die Störungsintensität am höchsten war. Vergleichbar dazu haben LOSOSOVÁ et al. (2012b) festgestellt, dass Lebensräume mit höherer Störungsintensität biotisch homogener sind. Obwohl in unserer Studie der Anteil nicht-einheimischer Arten eher niedrig war, konnten sich durch die Isolierung der Habitate in Kombination mit verarmten Samenbänken bzw. niedrigen Verbreitungspotenzialen kaum typische Arten des halbnatürlichen Graslands ansiedeln (NOVÁK & KONVIČKA 2006). Der Anteil von Arten des halbnatürlichen Graslands, z. B. *Achillea collina*, *Agrostis stolonifera*, *Astragalus cicer*, *Poa pratensis* und *Potentilla recta*, war im Grasland am Stadtrand (mittlere Sukzessionsstadien) signifikant erhöht.

Unsere Ergebnisse zeigen, dass die Artenzusammensetzung urbaner Graslandhabitate vom habitatspezifischen Störungsregime, abiotischen Faktoren und ihrer Entstehungsgeschichte beeinflusst werden (s. a. LOSOSOVÁ et al. 2012a). Die typischen Umweltbedingungen in urbanen Habitaten fördern eine Homogenisierung der Flora, die in den Stadtparks am stärksten ausgeprägt ist. Obwohl die Flora des urbanen Graslands in unserer Studie hauptsächlich aus angepassten Generalisten bestand, beherbergen solche Habitate oftmals die letzten Reste der ehemals weiter verbreiteten Graslandgesellschaften, die anderenorts der Intensivierung der Landnutzung zum Opfer gefallen sind. Urbanes Grasland kann damit wichtige Ökosystemdienstleistungen für Stadtbewohner erfüllen. Zudem kann urbanes Grasland eine wichtige Ressource für Renaturierungsprojekte bieten.

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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.

Appendix E1. Mean cover scores, frequency, relative indicator values for temperature, moisture and nitrogen, social behaviour type and the flora element type of the detected species in vacant lots (cover > 0.5%).

Anhang E1. Mittlerer Deckungsgrad, Stetigkeit, relative Zeigerwerte für Temperatur, Feuchte und Stickstoff, Strategietyp und Florenelementtyp der auf unbebauten Grundstücken festgestellten Arten mit Deckung > 0,5%.

Appendix E2. Mean cover scores, frequency, relative indicator values for temperature, moisture and nitrogen, social behaviour type and the flora element type of the detected species in urban parks (cover > 0.5%).

Anhang E2. Mittlerer Deckungsgrad, Stetigkeit, relative Zeigerwerte für Temperatur, Feuchte und Stickstoff, Strategietyp und Florenelementtyp der in den Stadtparks festgestellten Arten mit Deckung > 0,5%.

Appendix E3. Mean cover scores, frequency, relative indicator values for temperature, moisture and nitrogen, social behaviour type and the flora element type of the detected species in peri-urban grasslands (cover > 0.5%).

Anhang E3. Mittlerer Deckungsgrad, Stetigkeit, relative Zeigerwerte für Temperatur, Feuchte und Stickstoff, Strategietyp und Florenelementtyp der im Grasland am Stadtrand festgestellten Arten mit Deckung > 0,5%.

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