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Urban structure and environment impact plant species richness and floristic composition in a Central European city

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Abstract
Cities represent enviroment for most of Europe's human population. Spatial pattern of cities' environmental as well as socio-economic features affect plant biodiversity. We analysed a floristic mapping dataset of the city of Ljubljana (Slovenia) and asked what affects the spatial differences in the presence of different categories of species: species according to residence time and endangered and thermophilic species. To explain the proportions of these species groups in grid cells, using Generalized Additive Models, we tested the effects of three categories of predictors: i) urban structure, represented by the distance from the city centre, population density, soil sealing, and quality of residential environment index, ii) habitat predictors, represented by habitat diversity and geologic diversity, and iii) environmental conditions, represented by urban heat island (UHI). Species richness decreases with the distance from the city centre and is highest in the cells with intermediate habitat diversity. Number of species is highest within city parts of highest quality of residential environment index and lowest in parts with UHI effect. Proportion of native species is positively related to habitat and geologic diversity. The proportion of archaeophytes is higher where habitats are more diverse and increases with the distance from the city centre. Grid cells with highest proportion of neophytes are located in the most built-up areas and in the city centre, which is positively associated with soil sealing, but negatively with UHI. Thermophilic species are positively associated with soil sealing. Endangered species have uniform distribution pattern and their proportion is negatively associated with distance from the city centre and soil sealing. A grid cell with the highest proportion of endangered species includes two protected areas with wetland habitats. Calculated ecological indicator values show correlation with soil sealing and habitat diversity. Some of the results are in line with well-established patterns from other cities, while others reflect certain specific features of Ljubljana, e.g. forested hills close to the city centre. The identified hotspots of city's plant species richness can serve in the argumentation of future urbanistic planning.

Keywords Urban flora · Central Europe · Alien

Introduction

In Europe about three quarters of population live in urban and peri-urban areas (The World Bank 2020) and for majority of that population urban ecosystems are the only surrogate for nature that they are regularly in contact with (Endlicher 2012). Urbanization is a process of changing natural or rural landscapes to urban and is considered as one of the main reasons for loss of biodiversity (Gregor et al. 2012). But despite decline of native species populations (Aronson et al. 2015) a special flora develops in urban areas which is different from surroundings (Kowarik 1992) because of special ecological conditions (Wittig 2008) and enrichment in alien species (Celesti-Grapow et al. 2006).

Urban agglomerations and habitats within have specific site conditions compared to surrounding environment: increased temperature (urban heat island in the city) and rainfall (Ajaaj et al. 2018, Bornstein and Lin 2000), pollution (Ulpiani 2021), impervious surfaces (Salinitro et al. 2018), habitat fragmentation and disturbance (Kowarik 2011; Liu et al. 2016). Specific ecological factors are responsible for spatial distribution pattern of plants. UHI (urban heat island)

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phenomenon as characteristic indicator of urban environment is defined as metropolitan area significantly warmer than its surroundings. Usually it is well expressed in city centres with distinctly higher proportion of thermophilic species (Čeplova et al. 2017a; Schmidt et al. 2014).

Urban ecology is a term used for almost a century and in Central Europe its development started about half a century ago (McDonnell 2011). Urban flora (and vegetation) have been sampled for centuries (Gregor et al. 2012), but with different methodology and intensity (Pyšek 1995; Wittig 2008). First only floristic lists of species were compiled, and only later grid based surveys of whole cities were made (Celesti-Grapow 1995; Godefroid 2001; Landolt 2001; Martini 2010; Schmidt et al. 2014; Stešević and Jovanović 2008). Grid cell sizes differ between different studies from 0.1 km^2 (Trieste), to 1.6 km^2 (Rome), but most widely used size is 1 km^2. Size of grid cells varies according to aims of the study, and also size of the studied city, but it is always a trade-off between the precision and sampling effort (time). It also determines different sampling accuracy and one must be aware of shortcomings. However, grid based flora sampling is commonly associated by environmental and social data (Altobelli et al. 2007; Bechtel and Schmidt 2011; Schmidt et al. 2014). Recently research of urban flora focused on comparison of different habitats within urban settlements (Čeplova et al. 2017a; Kantsa et al. 2013; Lososová et al. 2012). Nevertheless, grid mapping is useful to detect ecological patterns in cities. Different approaches can give different results, sometimes even contradictory, but enable us to extract general patterns of urban floristic diversity. Urban settlements differ in their location, size, form and composition (Hough 1989; Luck and Smallbone 2010; Parker 2015), and most have certain features that cause some modifications of general floristic patterns in city floras.

Species richness differs within urban area and along urban–rural gradient. Plant species pool consists of indigenous species present in the area, indigenous colonizers and alien plants (Williams et al. 2009; Aronson et al. 2016) and they are filtered through urban drivers: habitat transformation and fragmentation, urban environment and human preferences. Last filter is mostly linked to introduction and persistence of alien species. Plant species richness increases from low to moderate urbanization, while species number decreases towards high urbanization (McKinney 2008). Spatial distribution of species richness and composition within a city is not strictly linked to centre-periphery gradient but is a result of complex mosaic of spatial and temporal drivers (Ramalho and Hobbs 2012).

In this context city Ljubljana can be considered as a perfect case study example for studying distribution of flora related to different abiotic and biotic factors. Particular feature of Ljubljana is ridge consisting of three hills running through the city as a green corridor in a NW–SE direction, making a natural forest corridor between neighbouring landscape units (Pirnat 1997). The city has experienced rapid development since the 1990s resulting in new multi-dwelling private housing development on brownfields (e.g. former barracks of the Yugoslav Army) or on derelict urban land (mainly reserved for industrial development in 1980s), development of new shopping centres, completion of the city ring around the inner-city of Ljubljana, and residential and commercial sprawl at the periphery of the inner-city area or in suburban municipalities (Pichler-Milanović and Lamovšek 2010).

Objectives:

- What are main environmental factors influencing species richness within Central European city (Ljubljana)?
- What patterns can be observed in urban agglomeration, based on species richness and species characteristics?

Methods

Study area

Ljubljana is the capital of Slovenia with approx. 300,000 inhabitants. Municipality of Ljubljana covers 274.99 km^2 (City of Ljubljana 2018) and many periurban areas are included (40% of the area is covered by agricultural land and 39% of forests). Average annual temperature is 10.9° C (climatological average 1981–2010) and average annual precipitation (1981–2010) is 1,363 mm (ARSO 2018).

Our study area was limited to area within the Ljubljana Ring Road representing urban area and covering 56.5 km^2 (Fig. 1). This area is characterized by three forested hilly areas (Rožnik, Grad, and Golovec) in the west and southeast with river Ljubljanica passing between them. The rest comprises more or less built up areas, gradually replaced by agricultural areas in some of the suburbs.

Area of today's Ljubljana was inhabited already in 13th century BC with its peak in 10th and 7th century BC. Romans later established important urban settlement Emona and the area was since then permanently populated (Ferle 2018).

Sampling

Floristic sampling of spontaneous flora started in 2015 and was based on a systematic grid of 1 km^2 cells covering the area within the Ljubljana ring road. Such sampling plan yielded 70 quadrats, in those with the ring road including the whole area to ensure comparability. Each cell was visited at least three times (spring, summer, autumn) to obtain all phenological stages and to avoid biased sampling. Within each cell all spontaneous (not cultivated) vascular flora was recorded. Sampling was done by team of University of Ljubljana. Data from the vegetation survey of Ljubljana made

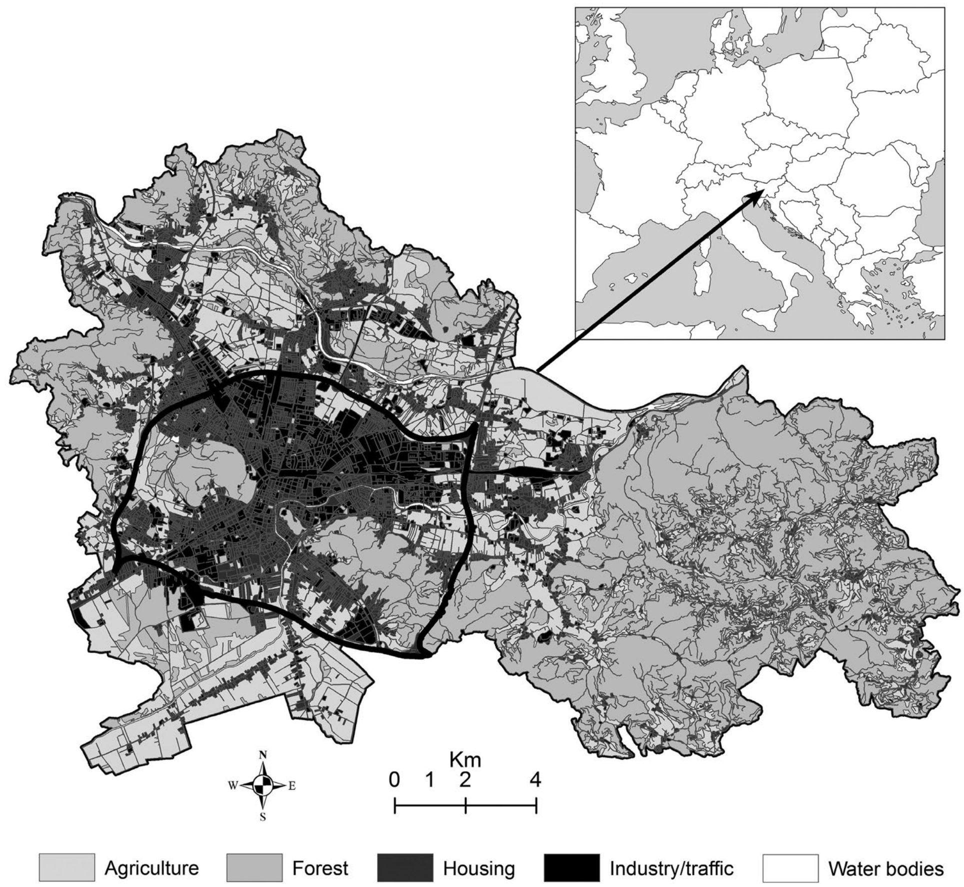

Fig. 1 Location of Ljubljana and land use map of municipality. Black line marks Ljubljana Ring Road

by researchers of ZRC SAZU was added and final dataset of floristic data from 1998 to 2018 was compiled and used in further analyses. It comprises 1200 plant taxa (roughly 1/3 of whole Slovenia's vascular plant flora).

Taxonomy and nomenclature of plant species are in accordance with Martinčič et al. (2007). Field records for some closely related taxa and those difficult for determination were aggregated at higher level of species or aggregates according to Martinčič et al. (2007), so that the final data matrix for further analyses comprised 1103 taxa by 70 grid cells.

Species traits and richness

Archeophytes are species introduced into Europe with Neolithic expansion of agriculture, while neophytes are species introduced after 1500 AD (Essl et al. 2018). For listing of archaeophyte and neophyte species we used expert opinion based classification, made for the whole flora of Slovenia by Jogan et al. (2012) and the report of the floristic mapping of Ljubljana by Jogan et al. (2015). As endangered we considered species listed on Slovenian Red list (Anonymous 2002) and/or list of protected species (Anonymous 2004–2014). As thermophilous we considered species with ecological indicator value (EIV) for temperature (Pignatti 2005) higher than 7 (Schmidt et al. 2014).

Ecological indicator values (EIV) as estimators of each species ecological requirements are used for estimation of site conditions and are a good surrogate for measured environmental variables (Diekmann 2003). Each plant species was assigned ecological values for climatic and edaphic factors using EIVs developed for Italy (Pignatti 2005) as the biogeographic conditions of study area are quite comparable to northern Italy. Based on species composition we calculated mean values for environmental conditions: light, temperature, moisture, continentality, soil reaction, and nutrients for each grid cell. Out of 1103 taxa we found available EIV's for 979 for light, 830 for temperature, 919 for continentality, 932 for moisture, 778 for reaction and 974 for nutrients. Ecological indicator values are very robust system and exclusion of less than 20% of the taxa from the species lists only weakly affects the average environmental indication values (Ewald 2003). For calculation of grid cell mean ecological indicator values (EIV) we used Juice software (Tichý 2002).

For each grid cell we calculated the absolute species richness, and proportions of native, archeophytes, neophyte, endangered and thermophilic species. Sample-based rarefaction curves were used to compare the numbers of native and non-native species between sampled grid cells. Rarefaction curves were made in Juice (Tichý 2002).

Environmental predictors

For description of environmental conditions and as factors potentially affecting species richness we used three categories of predictors. (i) Urban structure is represented by distance from the city centre, population density, soil sealing, and quality of residential environment index. (ii) Habitat predictors are habitat diversity and geologic diversity. Urban heat island structure represents (iii) environmental conditions. More detailed values of predictors for grid cells are shown in Table 1.

Distance from the city centre was calculated as distance from central square (Three bridges) to each grid cell centroid. Data on imperviousness (soil sealing) were obtained from dataset published by EEA (2018). Population density (nr. inhabitants/ha) and quality of residential

Table 1 List of predictor variables and descriptive statistics

		Mean	Std.Dev	Minimum	Maximum
Altitude (m)		309	26	277	398
Population density		27.93	24.19	0.00	110.46
Urban heat island		0.198	0.459	0.000	3.025
Soil imperviousness		33.45	22.50	0.02	84.42
Habitat diversity (% of area per grid cell)					
	Agricultural + Semi-natural areas + Wetlands	17.27	19.13	0.00	59.74
	Construction sites	0.33	1.23	0.00	8.21
	Continuous Urban Fabric (S.L. > 80%)	1.99	4.00	0.00	20.88
	Discontinuous Dense Urban Fabric (S.L.: 50%—80%)	15.96	14.78	0.00	54.46
	Discontinuous Low Density Urban Fabric (S.L.: 10%—30%)	0.85	1.34	0.00	5.79
	Discontinuous Medium Density Urban Fabric (S.L.: 30%—50%)	5.29	6.02	0.00	26.49
	Discontinuous Very Low Density Urban Fabric (S.L. < 10%)	0.00	0.01	0.00	0.11
	Fast transit roads and associated land	2.30	4.02	0.00	19.71
	Forests	19.22	30.00	0.00	95.77
	Green urban areas	2.82	4.47	0.00	22.57
	Industrial, commercial, public, military and private units	18.31	19.39	0.00	75.34
	Isolated Structures	0.12	0.28	0.00	1.26
	Land without current use	0.65	1.13	0.00	5.13
	Mineral extraction and dump sites	0.27	1.28	0.00	9.11
	Other roads and associated land	9.62	4.17	1.59	25.07
	Railways and associated land	1.59	4.24	0.00	23.62
	Sports and leisure facilities	2.32	5.04	0.00	32.52
	Water bodies	1.09	1.95	0.00	7.42
Distance from the city centre (m)		3308	1329	553	5876
Quality of residential environment index		-0.33	0.77	-1.73	1.35
Geologic diversity (% of area per grid cell)					
	Limestone	0.18	1.48	0.00	12.38
	Coarse-grained clastic deposit	49.00	44.43	0.00	100.00
	Fine-grained clastic sediments	32.87	42.83	0.00	100.00
	Sandstones, siltstones, claystones	17.87	31.07	0.00	99.43
	Various sediments	0.08	0.66	0.00	5.50
Mean Ecological indicator value					
	Light	6.58	0.26	6.00	7.03
	Temperature	5.92	0.21	5.42	6.26
	Continentality	4.89	0.08	4.70	5.00
	Moisture	5.11	0.34	4.46	5.91
	Soil Reaction	5.99	0.18	5.55	6.26
	Nutrients	5.38	0.16	4.95	5.70

environment index were extracted from Tiran (2017). The quality of residential environment index is calculated based on various elements of the residential environment arranged into groups: dwelling characteristics, safety, aesthetics, accessibility to urban amenities, environmental strain, social environment, and transportation conditions Tiran (2017). Urban heat island spatial structure has been produced with analyses of satellite thermography measurements (Landsat 8 imagery) that have adequate spatial resolution for a detailed analysis of land surface temperature variations. Analysis shows the frequency of occurrence of the top two percent of the highest temperatures in build-up areas in Ljubljana (Komac et al. 2016). All urban structure predictors were calculated in ArcGIS as mean per grid cell.

Habitat diversity was extracted from from Urban atlas land-use (EEA 2012) and 18 habitat (land-use) types were present in the study area. Data on geology were obtained from Basic geological maps (1:100 000) with 5 distinctive categories of geologic substrate (Geološki zavod Slovenije 2000). For habitat and geologic types we calculated the proportional area of particular categories for each grid cell in ArcGIS 10.4 (ESRI 2015). Further we calculated habitat and geologic diversity using Shannon–Wiener index (Schmidt et al. 2014).

Urbanization index

None of the variables representing urban structure, habitat, and environmental conditions solely accounts for urbanization. Therefore to present different degrees of urbanization within Ljubljana we calculated an urbanization index (Schmidt et al. 2014). We included data for soil sealing, population density, urban heat island and proportion of green areas per grid cell. Green areas were calculated as sum of proportions of following land-use categories: Agricultural + Semi-natural areas + Wetlands, Forests, Green urban areas, and Sports and leisure facilities. All predictors were standardized to mean zero values and index of urbanization is sum of all four standardized variables. The urbanization index was calculated as the sum of degree of soil sealing, population density, and urban heat island minus the proportion of green areas. For division of urbanization index we used "natural breaks" option in ArcGIS (Fig. 2).

Collinearity

We examined Spearman's correlation coefficients (Table 2) and the variance inflation factor (VIF) produced by CANOCO to diagnose and prevent collinearity among environmental predictors (Ter Braak and Šmilauer 2012). In case that VIF factor is higher than 10, the variable should be omitted from further analyses. None of predictors overcome this threshold so we used distance from the city centre, population density, soil sealing, quality of residential environment index, habitat diversity, geology diversity, and urban heat island in further analyses.

Generalized additive models (GAM)

To explain the spatial pattern of species richness, proportion of native and alien species and EIVs as a function of

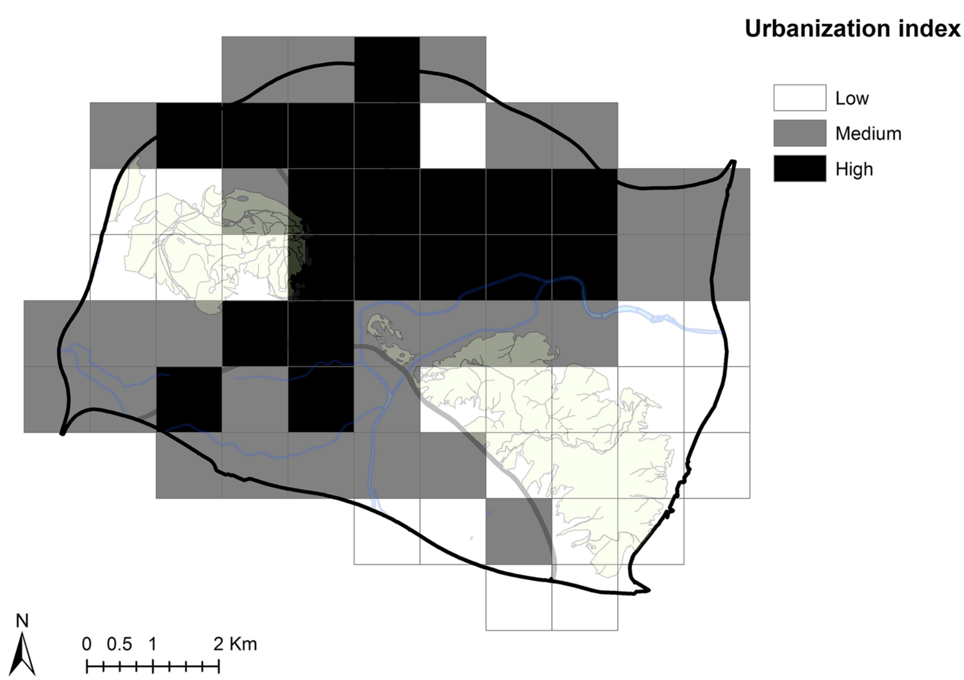

Fig. 2 Urbanization index in Ljubljana presented with three degrees (low, medium and high) divided by "natural break" function in ArcGIS

Table 2 Correlation matrix and VIF of all predictor variables included in the initial analyses: altitude, population density, soil sealing, urban heat island, distance from the centre, quality of residential environment index, habitat, and geologic diversity

	Altitude	Population density	UHI	Soil sealing	Distance	Quality of residential environment index	Habitat diversty	Lithology diversity	VIF
Altitude	1.000								3.4608
Population density	**-0.305**	1.000							2.7538
UHI	**-0.320**	**0.414**	1.000						1.7718
Soil sealing	**-0.342**	**0.774**	0.747	1.000					4.3472
Distance	-0.059	**-0.603**	**-0.278**	**-0.506**	1.000				2.1114
Quality of residential environment index	**0.508**	0.165	**-0.205**	-0.036	**-0.391**	1.000			1.5991
Habitat diversty	**-0.314**	**0.309**	0.181	**0.358**	-0.149	-0.061	1.000		2.7041
Lithology diversity	**0.656**	-0.230	**-0.489**	**-0.324**	0.048	**0.396**	0.021	1.000	1.5394

Correlations in bold are significant at $p < 0.05$

the selected predictors, we fitted generalized additive models (GAM) with degrees of smoothing to the data. We used Poisson distribution for count data and Gaussian distribution for the others. We used default smoothing method REML. All analyses were made with mgcv package (Wood 2015) in R (R Development Core Team 2012).

Given our sampling design with grid cells we tested for spatial autocorrelation (SA) using a Moran's I test. To correct for spatial autocorrelation we used Markov random fields in GAM.

Results

Flora of Ljubljana comprised 1103 plant taxa, with 845 native species, 173 neophytes, and 85 archaeophytes. Sixteen species (or species aggregates) were present in all grid cells: *Achillea millefolium* agg., *Bellis perennis, Cichorium intybus, Dactylis glomerata*, *Erigeron annuus, Glechoma hederacea, Plantago lanceolata, Plantago major, Poa annua, Potentilla reptans, Ranunculus acris* agg., *Sambucus nigra*, *Solidago canadensis*, *Trifolium pratense*, *Urtica dioica,* and *Verbena officinalis*.

The mean number of species per grid cell was 284 ± 38 (Table 3). There were no cells without alien species and also at least one endangered species was present in each 1 km^2 cell.

Sample-based rarefaction curves showed that cumulative species richness was highest for native species followed by neophytes and archaeophytes (Fig. 3). Archaeophytes richness quickly reached asymptotic value indicating the lowest dissimilarity between plant species composition for this species group.

Spatial patterns of variable values are very distinct (Fig. 4). Mean EIV for moisture shows clear north–south pattern with higher values in southern part with Ljubljana Moor and flora of ditches. Similar but less clear is distribution of mean EIV for nutrients, most probably a result of more intense agriculture in the southern part of study area. Indicator values for temperature are higher in built up areas and in the city centre, with lowest values in grid cells with forest vegetation. Spatial distribution of habitat diversity is less distinct, however, lower values coincide with very homogenous areas of forested hills, and the highest with grids, encompassing transitional areas between more natural and more urban habitats (foothills of hilly areas and on the south towards the Moor). Distribution of geological types clearly influences geological diversity. Geology is homogeneous in the NE (mostly old limestone pebble deposits of river Sava) and SW (mostly remnants of ancient lake that resulted in peaty and clay soils) in lowland areas and more diverse in grid cells including hills (contact of Quaternary sediments with Permian-Carboniferous sandstone and schist).

Spatial pattern of species richness is not very distinct (Fig. 5), however, grid cells with highest species richness are located on border between built up areas and forest habitats. Species richness decreases with distance from city centre

Table 3 Statistics of species richness values (total species number, number of neophytes, archaeophytes, native species, thermophilic species, and endangered species)

	Mean	Std.Dev	Minimum	Maximum
Nr. species	284.4	37.7	206	432
Natives	218.8	33.0	162	344
Archaeophytes	30.1	5.5	16	42
Neophytes	35.5	9.5	17	53
Thermophilous species	65.1	15.1	28	94
Red list species	5.6	2.5	1	16

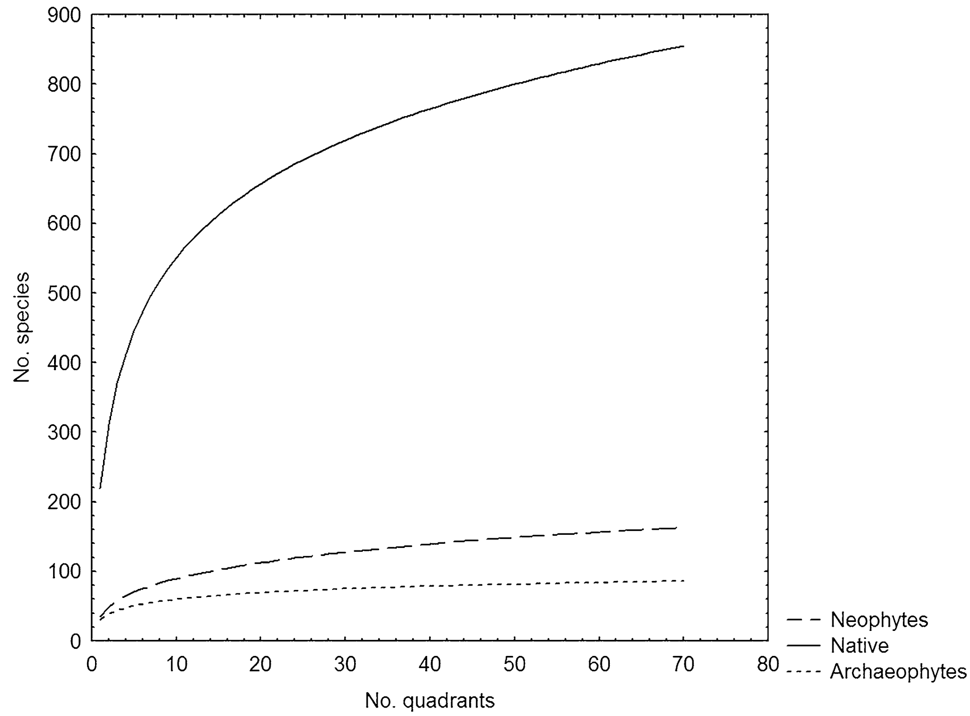

Fig. 3 Sample-based rarefaction curves indicating increase of cumulative number of native and alien species with increasing number of grid cells sampled

and is highest in cells with intermediate habitat diversity. Number of species is highest in city parts with highest life quality and lowest in parts with UHI effect (Table 4).

Spatial distribution of neophytes is related to urbanization pattern. Grid cells with highest percentage of neophytes have the highest proportion of built-up areas and are closer to the city center centre (Figs. 5 and 6). Additionally, this percentage is positively associated with soil sealing and habitat diversity, while negatively with UHI (Table 4). Proportion of archaeophytes is higher where habitats are more diverse and increases with distance from city centre. Relationships are reverse for native species. Very similar pattern could be observed in thermophilic species with lowest values in NW–SE direction. Thermophilic species are positively associated with soil sealing and negatively with geologic diversity (Table 4). Endangered species have a rather uniform distribution pattern and their proportion is (negatively) associated with distance from the city centre and soil sealing. Grid cell with highest proportion of endangered species that stands out includes two protected areas with wetland habitats (Fig. 5). Other grid cells with high scores for endangered species are also related to presence of well-preserved wetland habitat types, such as e.g. lowland river banks, wet meadows, native black alder carrs in wet valleys at the foothills.

Ecological indicator values show correlation mostly with soil sealing and habitat diversity. EIV for light, temperature and soil reaction are in positive correlation with these two factors, while moisture is in negative. EIV for light shows higher values in grid cells distant from city centre, while EIV for nutrients is lower in suburbs.

Discussion

In general, in city centres species richness is lower than in surroundings (Sudnik-Wójcikowska and Moraczewski 1998; Wittig 2010) regardless even of settlement size (Čeplova et al. 2017a). We found the opposing pattern in Ljubljana as number of species is decreasing with distance and coincides with higher urbanization index. Plant species richness depends also on other drivers not only urban–rural gradient from centre but also from the urban matrix of built up areas (Godefroid and Koedam 2007). Half open or open built-up areas promote the species richness and diversity. Similar process could also be rapid urbanization and rebuilding of cities after political changes in parts of Europe after 1990s that produced many open spaces, abandoned construction sites, and brownfields and consequently higher species richness. These special temporary habitats are quickly invaded by colonizers and harbour early and intermediate successional vegetation types that are otherwise not very common in most urbanized areas. Wastelands are the richest habitats in urban environment (Muratet et al. 2007).

Species richness

Largest floristic differences in Central European urban floras were observed between city centres and early successional and mid-successional habitats (Lososová 2011) with city centres being floristically very homogenous (Čeplova et al. 2017a). Grid cells with highest number of species in Ljubljana have also very heterogeneous land-use types on

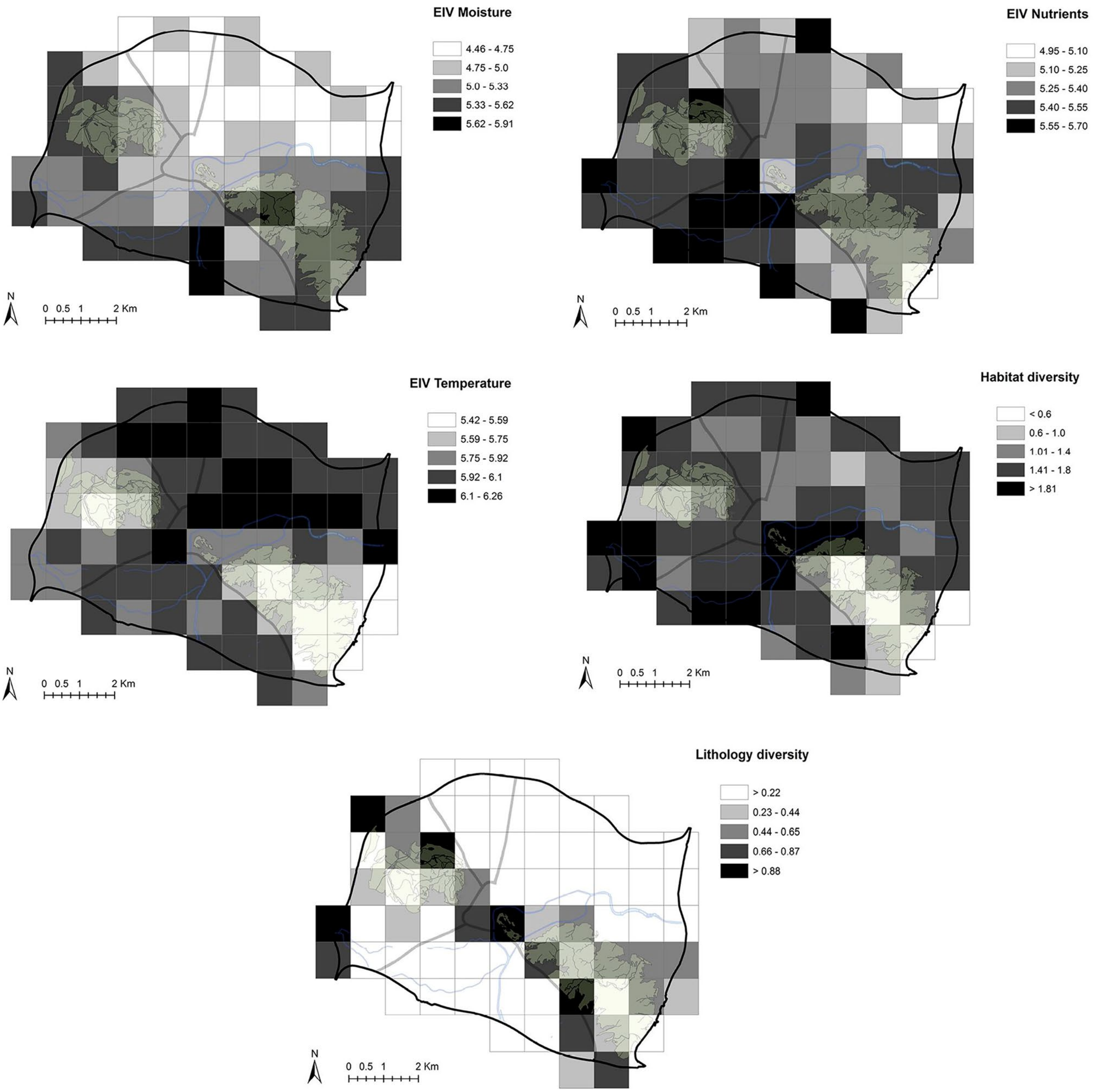

Fig. 4 Maps with average values for individual environmental and habitat predictors. Habitat and geologic diversity were calculated using Shannon–Wiener index

the border between urbanized areas and forests. High habitat diversity promotes high species diversity. Specific situation in Ljubljana is, that its centre encompases also hill of Ljubljana castle, with well-preserved natural habitat types on only 0,35 km^2.

Total species number is highest in parts of city with estimated best quality of residential environment. Species number is not necessarily good indicator of biodiversity but is used as a proxy for that. Higher biodiversity (species diversity and abundance) is often related to the quality of urban life (Adams 1994) and to higher number of ecosystem services (Železnikar et al. 2017).

Areas diverse in land use harbour more neophytes as they provide space for different species. Diversity of habitats is enhanced by presence of river corridors, gardens and abandoned lots which all act as source for neophytes in recent cities (Čeplova et al. 2017b; Kowarik 2010). In Ljubljana proportion of neophytes is positively related to soil sealing as a degree of urbanization which is consistent with general patterns of alien species distribution (Schmidt et al. 2014).

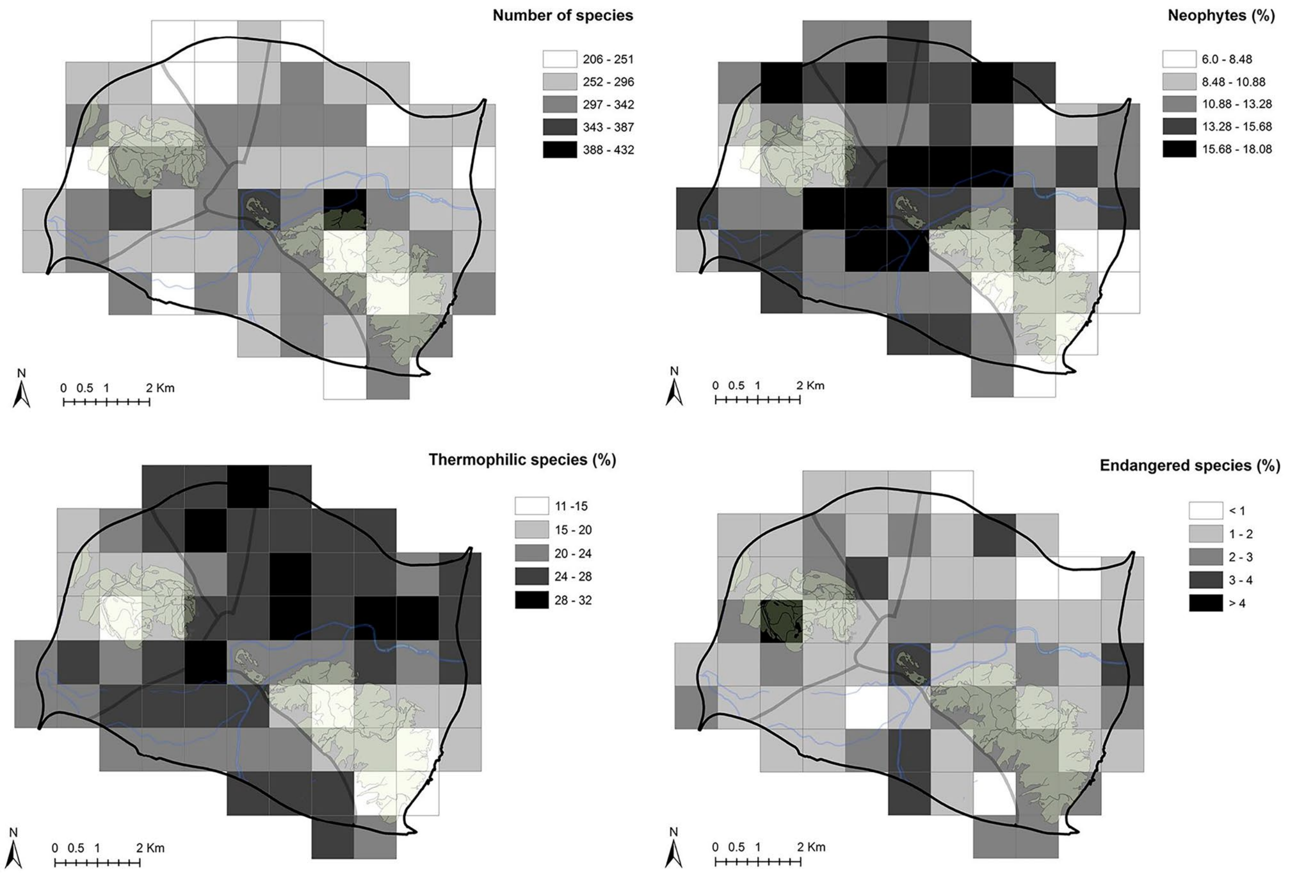

Fig. 5 Plant species richness within the Ljubljana ring road and their spatial distribution

Proportion of archaeophytes is higher in suburbs, but in areas with intermediate habitat diversity. This is in contrast with Lososová et al. (2012) who report more uniform distribution of archaeophytes across urban habitats although they are more common in early successional sites. But this could be the result of their specific sampling design not accounting for urban periphery with agricultural habitat types. Archaeophytes are generally more common in arable land (Küzmič and Šilc 2017) and are mostly annuals adapted to frequent and regular disturbance. Agricultural land is also distributed in the surroundings of cities and its specific arable flora contributes to the whole city flora.

Highest proportion of native species was found in grid cells with most homogeneous habitats and with less soil sealing, which are least changed by human activities. These grid cells are limited to forests within the study area where alien species are not able to penetrate (Chytrý et al. 2008; Küzmič and Šilc 2017; Wirth et al. 2020) due to known resilience of native forest vegetation.

Expectedly higher proportion of thermophilic species is related to soil sealing but it is surprising that relation to UHI areas is not significant. The core UHI in Ljubljana was estimated to comprise city centre (Jernej and Ramšak 2000) and at the end of twentieth century difference of 5 to 7 °C between highest (city centre) and lowest temperatures (outskirts) was observed (Jernej 2000). Specific and fast development of the city and in particular the construction of many shopping centres with large parking places to the northeast from the city centre increased the intensity of urban heat island phenomenon (Komac et al. 2016). Change and spread of UHI in Ljubljana is well supported by distribution of thermophilic species and EIV for temperature (Figs 4, and 5). EIV's and vascular flora already proved as a good UHI proxy (Bechtel and Schmidt 2011; Rysiak and Czarnecka 2018). In parts of the city with UHI increase in proportion of thermophilic species and archaeophytes is evident (Fig. 5). There are several thermophilous taxa that have not been recorded in the study area before (e.g. *Avena barbata*, *Catapodium rigidum*, *Rostraria cristata*, *Vulpia myuros* etc.), but appeared recently and are established. Many of them are common in the coastal region of Slovenia with sub-Mediterranean climate and the UHI effect which is more pronounced in the last decades, may explain their presence and establishment in Ljubljana.

Species are most often endangered due to human activities, therefore it is not surprising they are found in grids

Table 4 GAM of predictor variables on species richness and proportions.

	Nr. species	% natives	% archaeophytes	% neophytes	% thermophilic	% endangered	Light	Temperature	Continentality	Moisture	Soil reaction	Nutrients
Population	1.744	0.140	0.000	0.000	0.000	0.705	0.000	0.000	0.000	0.000	0.076	0.000
UHI	11.735***	0.123	0.465 *	0.708 **	0.000	0.000	0.235	0.000	0.000	0.000	0.000	0.264
Soil sealing	0.001	2.144 ***	2.536 ***	2.123 ***	5.392 ***	2.538 ***	2.773 ***	7.878 ***	3.058 ***	7.980 ***	2.443 ***	0.630 *
Distance	6.641 **	0.000	1.539 ***	0.532 *	0.000	0.558 *	0.816 ***	0.000	0.928 ***	0.000	0.937 **	0.336 *
Quality of residential environment index	15.535 ***	0.000	0.000	0.000	0.000	0.131	0.115	0.000	0.030	0.000	0.000	0.000
Habitat diversity	62.591 ***	1.538 ***	1.382 ***	0.761 **	3.738 ***	0.000	1.901 ***	5.188 ***	2.363 ***	0.000	3.587 ***	0.581 **
Geologic diversity	0.000	1.167 ***	0.236	0.796 **	1.905 ***	0.000	2.511 ***	3.297 ***	2.822 ***	0.000	3.984 ***	0.000
R-squared	0.378	0.682	0.795	0.564	0.784	0.308	0.763	0.849	0.705	0.793	0.733	0.436
Deviance explained	54	71.5	83.3	59.2	81.4	36	80.4	87.1	74.6	81.7	77.6	50.3

All values are F statistics apart from for Nr. species which are Chi-square. Significant codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

with low degree of soil sealing that represent more natural and less urbanized habitat types. Such semi-natural areas are frequently found in and around cities where endangered (and rare) species can survive (Kühn et al. 2004; Schmidt et al. 2014). In Ljubljana they are found in more marginal parts with wet plant communities such as bogs, carrs and standing water. Usually species preferring more acidic and cooler habitats are endangered or have already disappeared by urbanization (Knapp, 2009). It was not unexpected to find endangered species in grid cells with protected zones (Fig. 5) but they are common also in other urban area. Quite often also red list species are found in residential areas (Maurer et al. 2000) or surroundings as cities are often founded on pre-existing biodiversity hot-spots or areas with high geological diversity (Kühn et al. 2004).

Environmental factors

The most important environmental factors, determining total species number and species composition are habitat diversity and soil sealing (as the strongest factor reflecting the human impact), but also geologic diversity, distance from the city centre and UHI. Population density and quality of residential environment index did not affect the patterns of the observed variables much. Flooring type of streets influences species diversity of urban plants, with lowest species number on most sealed surfaces (Salinitro et al. 2018).

EIV are useful tool for description of environmental conditions and were used in many studies related to urban flora (for the review see Williams et al. 2015). Caution with interpretation is needed by using EIV's because of circularity (Zelený and Schaffers 2012) and comparison with much different vegetation types (Diekmann 2003) nevertheless ecological indicator values show a good match with environmental factors although they are not always unequivocal. For all indicator values influence of habitat diversity was significant and can be explained by the availability of different ecological niches in the same sampling area that enables presence of very different ecological groups of plants, among others also those with extreme ecological preferences. To study this phenomenon in detail, frequency distribution patterns of EIV scores within sampling areas would be better than just average values, but this was beyond our research scope. Urban areas are very diverse due to anthropogenic influence responsible for presence of wide spectrum of environments in small area (Gilbert 1989) and in such conglomerate of multiple stressors, detecting trends can be challenging (Williams et al. 2015).

EIV for moisture is negatively related to soil sealing as mostly species adapted to dry conditions can thrive on paved and asphalt surfaces. EIV moisture index was strongly significantly related only to densely built-up areas among all urban habitats (Godefroid and Koedam 2007).

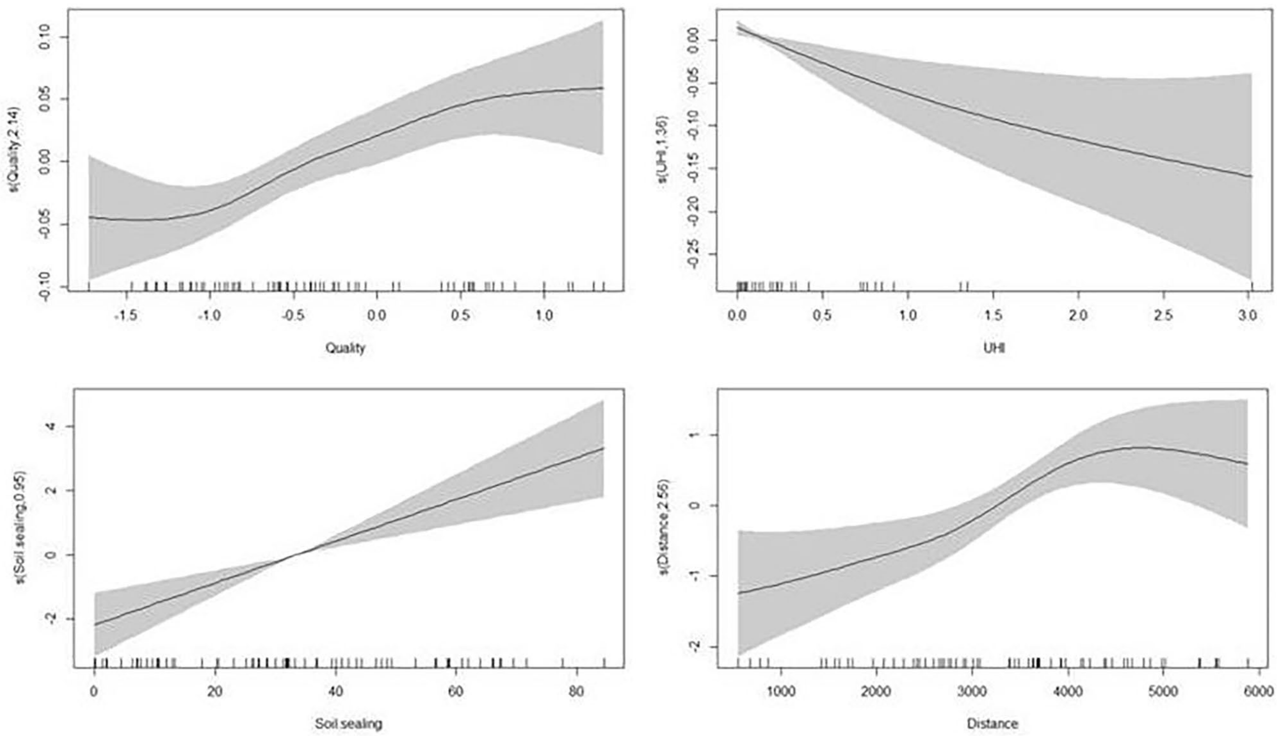

Fig. 6 Plots showing of GAMs for number of species (upper two) and proportion of neophytes (lower left) and archaeophytes (lower right) and various predictors

Additionally, EIV for continentality is positively correlated with soil sealing and negatively correlated with distance from the city centre, which could be explained by the common denominator – drought (Wittig 2008). Continental climate in European context as opposed to Atlantic climate, signifies hot summers with little rainfall, resulting in summer droughts. The same occurs on highly sealed soils (interrelated to the vicinity of city centre) due to water runoff and increased heat radiation that is more related to UHI phenomenon.

Expectedly EIV for temperature is also in positive relation to soil sealing (Williams et al. 2015), but unexpectedly no relationship was discovered with UHI pattern. It is possible that extreme UHI areas in Ljubljana are too small and dispersed in several parts of the city that obvious pattern was not revealed or they were not detected because of too coarse sampling grid.

Regarding cities, nitrogen concentration in soils is usually higher in city centres (Leuschner and Ellenberg 2017; Lovett et al. 2000) or in more urbanized landscape (Schmiedel et al. 2015; Wittig 2008). Williams et al. (2015) found in their synthesis strong support for the hypothesis that urbanization favours species with an affinity to high nutrient environments and our study confirms that.

More heliophilous species are increasingly found along urban–rural gradient. This contradicts other studies that found increase of light demanding species in the urban centres (Williams et al. 2015) or towns compared to villages (Šilc 2010). Explanation could be that on the outskirts of the Ljubljana are fields and grasslands and in other cases forests with shade-tolerant species. Mosaic of diverse habitats in periphery also promotes heliophilous species. General light intensity on its own is not higher in the city centre, however, higher amount of sealed soil possibly influences competition and enables light demanding species to be more frequent. In addition to that, a very specific light condition pattern in the city is a result of big vertical reflective surfaces of facades and glass covered buildings. And we have to bear in mind, that below huge city centre buildings there are several niches without direct sun radiation, watered by regular management, shadowed by trees, hidden in narrow backyards etc. where also several sciophytes can persist.

EIV for soil reaction increases towards the centre of the city (as does soil sealing) and this is supported by several studies (Williams et al. 2015). In Central Europe species are generally adapted to higher alkalinity because of widespread calcareous bedrock. Important reason for more alkaline soils in urban environment are disturbance but primarily release of calcium from mortar, cement, plaster and other components of building rubble (Forman 2014; Gilbert 1989). In Ljubljana periurban area soil reaction pattern is clearly linked to geological substrate: in the NE mostly old limestone pebble deposits of river Sava resulting in neutral to slightly alkaline soils, in SW remnants of ancient lake deposits with acid soils and similarly in the forested hills with siliceous base rock.

Peculiarities of Ljubljana

As mentioned previously there are already known general patterns of species distribution in urban environment (James 2010), but some particular characteristics of each city show special species distributions indicating those characteristics that are not linked to typical urbanization gradient. The first group of these characteristics is related (i) to natural conditions of the settlement and the other (ii) to sociological characteristics since the urban ecosystem is regarded as a complex social-ecological system (Pickett et al. 2001).

In Ljubljana the first group is represented by (i) a ridge consisting of three hills running through the city, and by (ii) the difference in the soil composition of alluvial plains in the north and south of the city. Forest vegetation and large parks are located mainly on hills and their foothills and consequently less neophytes and thermophilic species are found here. In general parks with their habitat diversity are considered to have large species pool, the total number of species present and are also important as species source (Forman 2014). Green spaces with semi-natural soils in urban areas are considered to have highest species diversity (Salinitro et al. 2018) and ornamental horticulture is major pathway alien plant introduction and spread (Van Kleunen et al. 2018). In Ljubljana several city parks are intensively managed with very frequent mowing of lawns and well maintained decorative shrubs and trees, so there is only little niche available for the spontaneous flora. In the range of 1 km walking distance around the city centre of Ljubljana and within urban areas of the city, forests comprise more than one quarter of the area (Hladnik and Pirnat 2011). Forests around Ljubljana on acidic silicate bedrock are comparably species poor, but otherwise forests are rich in species compared to other intensively managed urban green areas (Železnikar et al. 2017). Geological differences are also visible in flora of alluvial plains. Southern part harbours more indicator species for moisture and nutrient rich soils on finer sediments versus gravel sediments in the northern part.

Secondly, from sociological point of view, the city has been developing rapidly since the 1990s, that was caused by new political system related with urbanization of derelict urban land on brownfields, building of new peri-urban shopping centres, and residential and commercial sprawl at the periphery connected to suburban municipalities (Pichler-Milanović and Lamovšek 2010). Shopping centres are accompanied by extensive parking areas on the outskirts of the city centre, representing large areas of impervious soils, which distort the otherwise clear urban-suburban-rural gradient. More thermophilic species and neophytes are found in these habitats. This is in slight contradiction with decrease of alien species from city centre (Brunzel et al. 2009), but shopping areas could be seen as centres of urban settlement with soil sealing, high population density, traffic frequency as some characteristics of the urban area (Forman 2014; Wittig 2008). UHI is often highlighted as the most obvious manifestation of urbanization (Landsberg 1981), and higher temperatures were observed in these parts of Ljubljana (Komac et al. 2016).

Conclusions

Explaining biodiversity in urban landscape presents a great challenge, because in addition to environmental parameters a variety of socioeconomic, historical and urbanistic factors influence these patterns. We tested several groups of factors against patterns of different species groups and ecological indicator values in Ljubljana, capital of Slovenia. We found that as in many other cities, species richness decreases with the distance from the city centre, mostly due to construction sites, brownfields and natural/urban habitat heterogeneity, which all highly increase habitat variability. Socioeconomic characteristics also highly influence urban biodiversity patterns. Neophyte species are confirmed as urbanophilic, since in cities high habitat heterogeneity creates spaces for establishment and the propagule pressure is high. Native species on the other hand are more frequent in more natural habitats, which is also the case for the endangered species. Occurrence of thermophilic species is closely related to soil sealing (being one of the most important environmental factors predicting species numbers in general), which indicates higher urbanization levels. The presence of the associated Urban Heat Island phenomenon seems to be less and less restricted to city centres in the last decades due to new shopping centres and parking lots emerging prevalently on the cities' outskirts. In addition to general patterns on urban biodiversity, every city has its peculiarities that are governed by natural conditions of the settlement and its sociological characteristics. In the case of Ljubljana, the former include three forested hilly areas, which bring highly natural habitats almost to the city center, and different geological and soil composition in different parts. The latter include a rapid constructional development since the 1990's and large areas of densely built-up surfaces in the city's periphery. Future urbanistic planning will unavoidably influence the general patterns of urban biodiversity by maintaining, encouraging or diminishing main factors, contributing to high species richness and variability.

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Authors' contributions NJ concieved and lead the sampling, UŠ made statistical analyses and wrote the first draft of the manuscript, which FK and NJ critically and substantially edited. All authors read and approved the final manuscript.

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Consent for publication All authors agreed with the content and all gave explicit consent to submit.

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