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Trends in species diversity and composition of urban vegetation over three decades

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Abstract

Question: What was the change in diversity of urban synantropic vegetation in a medium-sized Central European city during the period of increasing urbanization (1960s-1990s)?
Location: The city of Plzeň, an industrial centre of the western part of the Czech Republic.
Methods: Sampling of various types of synanthropic vegetation, conducted in the 1960s, was repeated by using the same methods in the 1990s. This yielded 959 relevés, of which 623 were made in the 1960s and 336 in the 1990s. The relevés were assigned to the following phytosociological classes: *Chenopodietea, Artemisietea vulgaris, Galio-Urticetea, Agropyretea repentis* and *Plantaginetea majoris*. Total number of vascular plant species, evenness index J, number of alien species (classified into archaeophytes and neophytes), and mean Ellenberg indicator values for light, temperature, continentality, moisture, soil reaction, and nutrients were obtained for each relevé.
Results: From 1960s to 1990s, there was a significant decrease of species richness and diversity in synanthropic vegetation. The proportion of archaeophytes decreased in most vegetation types, indicating the contribution of this group of species, often confined to specific rural-like habitats, to the observed impoverishment of ruderal vegetation. The proportion of neophytes did not change between the two periods. Comparison between 1960s and 1990s indicated a decrease in light, temperature, moisture, soil reaction and nutrient indicator values in some vegetation types. In both periods, *Artemisieta, Galio-Urticetea* and *Chenopodietea* formed a distinct group harbouring more species than *Agropyretea* and *Plantaginetea*. Neophytes, i.e. recently introduced species, were most represented in the early successional annual vegetation of *Chenopodietea*, rather than in perennial vegetation of the other classes.
Conclusions: Synanthropic vegetation of Plzeň exhibited a general trend of decrease in species diversity.

Keywords: Biotic homogenization; Indicator value; Phytosociology; Plant invasion; Ruderal vegetation; Synanthropic; Temporal trend.

Nomenclature: Ehrendorfer (1973) for species; Moravec et al. (1995) for phytosociological units.

Introduction

Flora and vegetation of cities are different not only from semi-natural and natural vegetation but also from human-made habitats outside cities (Kowarik 1988). Although numerous studies were devoted to human-made habitats in open landscape (Prach et al. 1997; Sýkora et al. 2002), the main focus is on vegetation of large urban agglomerations (Pyšek 1993; Kowarik 1995). Cities have their own spatial organization and distinctive patterns of change through time, which result in patterns of species behaviour, populations dynamics and the formation of communities, each of which is specific to the urban environment (Sukopp 2002). The unique character of urban habitats was well demonstrated after World War II; less than three years after the ‘Blitz’, Salisbury (1943) described plant species that colonized the ruins in London, and in many cities war damage and its effects gave rise to studies of rubble flora and fauna (Sukopp 2002). Later on, vegetation of a number of cities has been described in remarkable detail by using phytosociological methods (e.g. Kopecký 1980-1984; see Wittig 2002 and references therein) but the generalizations yielded by such studies were rather limited, given the descriptive nature of sampling and lack of statistical methods used (Wiegleb 1986).

Flora of urban habitats has long been recognized as considerably rich in species. Cities represent an accumulation of species diversity in intensively managed landscapes (Haeupler 1974; Kühn et al. 2004). This is due to a high heterogeneity of the urban environment which provides plants with habitats convenient for all kinds of strategies (Gilbert 1989). Urban flora is also significantly enriched by invasions of alien species, the proportion of which in Central European cities varies between 20-60%, with a mean value of 40% (Pyšek 1998; 54 cities). The proportion of non-native taxa in urban floras increases with city size (Klotz 1990; Pyšek 1998), hence the phenomenon of high species diversity is more pronounced in large industrial cities (Pyšek 1993). It was recently pointed out that cities are naturally species-rich in native species due to their heterogeneous geological substrate, which is on average more diverse than a randomly selected landscape section in the surrounding area (Kühn et al. 2004). This makes their flora prone to the loss of native species, spread of aliens, and thus biotic homogenization (McKinney & Lockwood 1999; Olden et al. 2004).

Comparisons of changes in richness and composition of urban flora over time have been so far limited to the scale of entire cities. For several European cities, floristic lists from the 19th century were compared with the recent situation, e.g. for Halle (Klotz 1987), Leipzig (Klotz & Gutte 1992), Zürich (Landolt 2000) and Plzeň (Chocholoušková & Pyšek 2003). These studies yielded knowledge on the long-term dynamics in species richness and shifts in representation of particular life forms and life strategies, and some of them also indicated, by using Ellenberg indicator values (Ellenberg et al. 1991), changes in environmental conditions. However, no such systematic comparison was made at a smaller scale, e.g. for vegetation types occurring in urban sites. Studies on vegetation dynamics in cities are limited to recording the course of succession in permanent plots (Pyšek 1977) that are able to cover only a small part of variation of urban vegetation. The present study is novel in that the extensive sampling of vegetation of the city of Plzeň, conducted in the 1960s (Pyšek 1978), was repeated by using the same methods after three decades.

The background of the present study is a hypothesis that in spite of the high species richness of urban environments, increasing urbanization pressure leads to species-compositional and/or functional homogenization of urban landscapes. It is aimed at answering the following questions: Are there any changes in species richness and evenness over the last thirty years? What are temporal trends in the representation of alien species over the study period? Do these changes differ among vegetation types? What is the variation in species richness and evenness among particular habitat types? Are there any habitat changes that can be detected by indicator values?

Methods

Study area

The city of Plzeň (49°45'N, 13°23'E), an industrial centre in the western part of the Czech Republic, is located at the confluence of four rivers at an altitude of 310-380 m. Mean annual temperature is 7.8°C, annual sum of precipitation is 524 mm (Vesecký 1961, 50-yr average). The number of inhabitants increased from 86 000 at the beginning of the 20th century to 148 000 in the 1960s to 165 000 in the 1990s, and the proportion of built-up area increased in the last three decades (see map in Chocholoušková & Pyšek 2003). From a botanical viewpoint, Plzeň represents one of the most thoroughly studied cities not only in the Czech Republic but also in Europe. There are detailed overviews of vegetation and flora in both ruderal habitats of the city centre and semi-natural sites at the periphery (Pyšek 1974; Pyšek & Pyšek 1988; Nesvadbová & Sofron 1997).

Vegetation sampling

Vegetation relevés were recorded by using the Braun-Blanquet seven-degree scale of abundance and dominance (Westhoff & van der Maarel 1978), adopting the same methods both in the 1960s (Pyšek 1978) and 1990s. All relevés were recorded at the territory of the city of Plzeň, but not in the same plots, due to difficulties of preserving permanent plots in a highly dynamic city environment over several decades.

In both periods, vegetation sampling focused on spontaneously developed herbaceous vegetation in man-made or heavily disturbed habitats. Habitats on water-logged soils and vegetation stands with predominance of meadow or dry grassland species were excluded. Sampling in the 1960s aimed at documenting as many associations of the traditional Braun-Blanquet phytosociology as possible; therefore a wide range of habitats and vegetation types was covered. A total of 959 relevés of plots of 1 to 25 m^2 were recorded, of which 623 were made in 1960-1969 by A.P. and 336 in 1996-2002 by Z. C.; the comparability of data from both periods was achieved by conducting the 1990s research under the supervision of A.P. The relevés are stored in the Czech National Phytosociological Database (Chytrý & Rafajová 2003) under the nos. 536947-537986. Data editing and relevé analysis were managed in the JUICE program (Tichý 2002). Only vascular plants were considered, as other plant groups play an insignificant role in the studied vegetation.

The following information was included:

1. Year of the record, converted to one of the two periods (further termed 1960s and 1990s).
2. Relevé area in m^2 as originally recorded.
3. Phytosociological class. In order to account for possibly different trends of vegetation change in different habitats, we classified the whole data set by cluster analysis from the PC-ORD 4 package (McCune & Mefford 1999). We calculated relative Euclidean (chord) distance for square-rooted percentage cover data and applied the β-flexible clustering method with $\beta = -0.25$. We accepted five clusters at the highest hierarchical

level, which roughly corresponded to the following phytosociological classes (see Fig. 2 for numbers of relevés in the 1960s and 1990s):

Chenopodietea – annual synanthropic vegetation; $n = 536$;
Plantaginetea majoris – annual or perennial vegetation of trampled habitats; $n = 189$;
Galio-Urticetea – perennial synanthropic vegetation of mesic habitats; $n = 124$;
Artemisietea vulgaris – perennial synanthropic vegetation of xeric habitats, $n = 74$;
Agropyretea repentis – perennial vegetation of disturbed loamy soils; $n = 34$;

A shortened synoptic table of this classification is presented in App. 1. In this table, diagnostic species were defined on the basis of their fidelity to particular clusters. Fidelity was measured on presence/absence basis, using the phi coefficient of association (Sokal & Rohlf 1995; Chytrý et al. 2002). Species with $\Phi > 0.12$ were accepted as diagnostic.

4. Total number of vascular plant species in a relevé.

5. Evenness index J calculated as $H'/\ln S$, where H' is the Shannon diversity index and S is the number of species. H' (e.g. Magurran 1988) was calculated after transformation of the Braun-Blanquet scale values to percentage cover: r = 0.1%; + = 1.0%; 1 = 2.5%; 2 = 15.0%; 3 = 37.5%; 4 = 62.5%; 5 = 87.5%.

6. Number of native and alien species in a relevé. Alien species were classified as archaeophytes (immigrated in the territory of the present Czech Republic before 1500) and neophytes (immigrated after 1500) according to Pyšek et al. (2002).

7. Mean Ellenberg indicator value for light, temperature, moisture, continentality, soil reaction, and nutrients (Ellenberg et al. 1991) based on species presence, i.e. unweighted by their cover-abundance values.

Statistical analysis

Total number of species and numbers of archaeophytes and neophytes were square root transformed (where zero scores of archaeophytes and neophytes were first transformed to 0.5). Proportions of neophytes and archaeophytes were angular transformed, and area was $\log_e$ transformed. The appropriateness of the transformations was checked by the Box-Cox method (Box & Cox 1982), by plotting standardized residuals against fitted values, and by normal probability plots (Crawley 1993). Homogeneity of variances was checked by Levene's test. For non-significant intermediate levels of mean squares, pooling rules proposed by Bancroft (1964) were followed.

Species-area relationships were evaluated by completed ANOVA tables with regressions, and by tests of equality of regression slopes, following Sokal & Rohlf (1995). Because these relationships differed between the 1960s and 1990s, it was necessary to remove the effect of plot size (Chytrý 2001). Analyses potentially affected by species-area relationships were made only for 10 m^2 plots, i.e. the most frequent plot size. Analyses of the proportion of archaeophytes were made for all relevés and classes, because the effect of plot size on the proportional representation of archaeophytes was non-significant.

Temporal trends were evaluated by factorial ANOVAs with disproportional and unequal sample sizes, using periods and phytosociological classes as fixed effects. The analyses were made by an iterative approximate estimation technique in SPSS (Release 11.0.1. Anon. 2001), using univariate general linear models with type III sum of squares. Multiple comparisons of differences among classes were made by LSD tests.

Changes in habitat conditions between 1960s and 1990s based on Ellenberg indicator values of individual species were evaluated by one-way ANOVAs. Because the frequency of individual classes in the relevés significantly differed between 1960s and 1990s (G-test on contingency table: $\chi^2 = 38.94$; df = 4; $P < 0.001$), the changes were evaluated separately for each class.

Results

Species-area relationships

The total number of species significantly increased with relevé area in both periods (Table 1) but significantly faster in 1960s than 1990s ($F = 14.34$; df = 1, 28; $P < 0.001$). The square-rooted species-log area relationship for the total number of species in 1960s significantly deviated from linearity (Table 1). Relationships of other community characteristics to relevé area did not provide consistent results and are not presented here.

Table 1. Completed ANOVA tables with regressions of the species-area relationships for the total number of species in the 1960s and 1990s. *** $P < 0.001$; ** $P < 0.01$; ns = not significant.

	1960s			1900s		
Source of variation	df	MS	F_s	df	MS	F_s
Among area	14	4.80	0.43 ns	16	1.83	0.16 ns
Linear regression	1	58.78	90.44 ***	1	17.61	22.55 **
Deviations	13	0.65	2.55 **	15	0.78	1.39 ns
Within area	608	0.25		319	0.56	

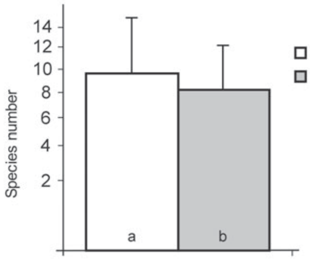

Fig. 1. Means (with standard deviations) of the total number of species in 10-m^2 relevés in the 1960s and the 1990s. Different letters inside the bars indicate significant differences ($P < 0.05$) between the 1960s and the 1990s (Table 3). Sample sizes are $n = 259$ for 1960s and $n = 167$ for 1990s. Note the square-root transformation of values on the vertical axis.

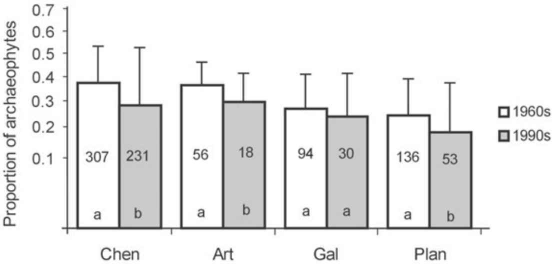

Fig. 2. Means (with standard deviations) of the proportions of archaeophytes in the phytosociological classes in all relevés in 1960s and 1990s. Chen = *Chenopodietea*; Art = *Artemisietea*; Gal = *Galio-Urticetea*; Plan = *Plantaginetea*. The *Agropyretea* are not presented because of small sample size in the 1990s ($n = 4$). Different letters inside the bars indicate significant differences ($P < 0.05$) between the 1960s and the 1990s (Table 3). Figures inside the bars are sample sizes. Note the angular transformation of values on the vertical axis.

Temporal trends in species diversity and representation of alien species

Mean total number of species per relevé was significantly higher in 1960s (11.5 ± 4.8, $n = 259$; mean±SD) than in the 1990s (9.4 ± 3.9, $n = 167$) (Table 2, Fig. 1). The same yet insignificant temporal trend, i.e. decrease from the 1960s to the 1990s, was observed for the number of archaeophytes (4.4 ± 1.6 and 3.6 ± 2.6) and evenness (0.61 ± 0.20 and 0.57 ± 0.10), respectively. The number (1.1 ± 1.6 and 1.0 ± 1.3) and proportion of neophytes (0.09 ± 0.20 and 0.09 ± 0.10, respectively) did not change from the 1960s to the 1990s.

The value of the Shannon index significantly decreased from 1960s to 1990s and the trend was consistent regardless of vegetation type (the effect of period on the value of Shannon index in two-way fixed effect factorial ANOVA with disproportional and unequal sample sizes: F = 12.25; df = 1, 416; $P = 0.001$; the effect of interaction between periods and phytosociological classes: F = 1.42; df = 4, 416; ns).

Temporal trends did not differ among phytosociological classes with the only exception of the proportion of archaeophytes, indicated by a significant period × class interaction obtained for this characteristic (Table 2). This significant interaction resulted from an increase in the proportion of archaeophytes in *Agropyretea* (F = 4.78; df = 1, 32; $P < 0.05$) where, however, only four samples were available in the 1990s (Fig. 2), and from an insignificant decrease in *Galio-Urticetea* (F = 1.37, df = 1, 62; ns). In the other classes, a significant decrease in the proportion of archaeophytes from 1960s to 1990s was observed, i.e. *Artemisietea* (one-way ANOVA: F = 7.55; df = 1, 72; $P < 0.01$), *Chenopodietea* (F = 35.64; df = 1, 536; $P < 0.001$) and *Plantaginetea* (F = 8.067; df = 1, 187; $P < 0.01$).

Species number, evenness and representation of alien species in ruderal vegetation types

Total species number (Fig. 3A) and number of archaeophytes (Fig. 3B) were significantly higher in *Galio-Urticetea*, *Artemisietea* and *Chenopodietea* than in *Agropyretea* and *Plantaginetea*. The number (Fig. 3C) and proportion (Fig. 3D) of neophytes were significantly higher in the *Chenopodietea*, dominated by annuals. *Agropyretea* and *Chenopodietea* exhibited the lowest eveness and significantly differed from the other classes, whose eveness values were not significantly different from each other (Fig. 3E).

Table 2. Two-way fixed effect factorial ANOVAs with disproportional and unequal sample sizes for periods and phytosociological classes. The main effect of proportion of archaeophytes was not tested because the interaction was significant. *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$; ns = not significant.

		Total number of species		Number of archaeophytes		Number of neophytes		Proportion of neophytes		Evenness		Proportion of archaeophytes		
Source of variation	df	MS	F_s	MS	F_s	MS	F_s	MS	F_s	MS	F_s	df	MS	F_s
Period	1	3.31	9.85 **	0.99	3.78 ns	0.078	0.49 ns	0.004	0.11 ns	0.059	3.64 ns	1	0.039	
Phytosociol. class	4	2.91	8.68 ***	4.71	17.93 ***	1.78	11.05 ***	0.34	9.53 ***	0.14	8.53 ***	4	0.69	
Period × class	4	0.71	2.10 ns	0.62	2.37 ns	0.21	1.33 ns	0.083	2.30 ns	0.016	1.02 ns	4	0.087	2.54 *
Error	416			0.26		0.16		0.036				949		

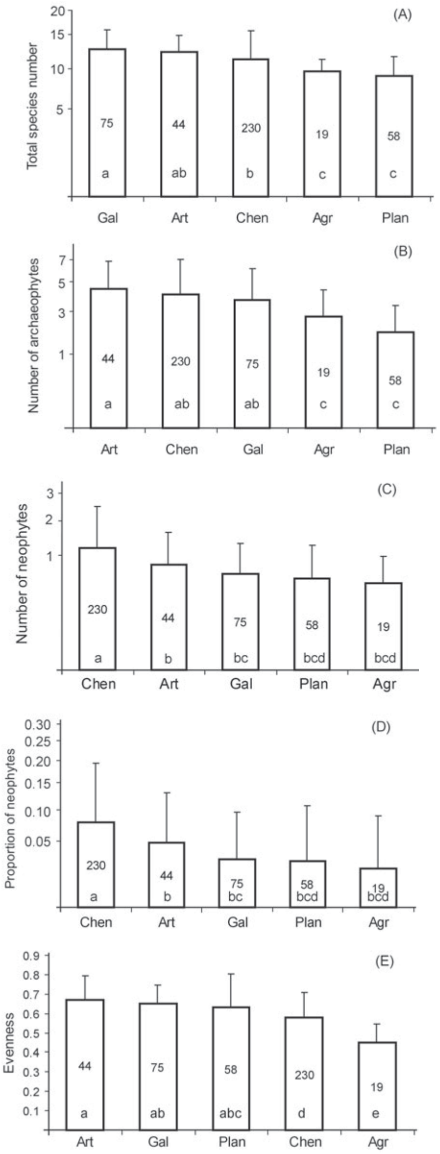

Fig. 3. Differences among mean values (with standard deviation) of phytosociological classes for (**A**) the total number of species; (**B**) number of archaeophytes; (**C**) number of neophytes; (**D**) proportion of neophytes; (**E**) evenness. Different letters inside the bars indicate significant differences ($P < 0.05$) among the phytosociological classes in LSD tests. Figures inside the bars are sample sizes. Class codes as in Fig. 2. Note the square-root or angular transformation of values on the vertical axes in numbers or proportions, respectively.

Table 3. One-way fixed effect ANOVAs for proportion of archaeophytes in 1960s and 1990s among classes.
*** $P < 0.001$; ** $P < 0.01$.

Source of variation	1960s			1990s		
	df	MS	F_s	df	MS	F_s
Among classes	4	0.74	33.02 ***	4	0.22	3.97 **
Error	618	0.023		331	0.057	

For the proportion of archaeophytes, where a significant period × class interaction was detected (Table 2), differences among phytosociological classes had to be evaluated separately for the 1960s and 1990s (Table 3). Both in the 1960s and 1990s, the proportion of archaeophytes did not differ significantly in *Galio-Urticetea* and *Plantaginetea*; in the latter class, this proportion was significantly lower than in the other classes. *Chenopodietea* and *Artemisietea* had a higher proportion of archaeophytes than the other classes in the 1960s, but not in the 1990s (Fig. 4).

Changes in habitat conditions

Indicator values that significantly differed between the two periods were always higher in 1960s than in 1990s. Light and temperature significantly decreased in *Chenopodietea*, continentality in *Artemisietea*, *Chenopodietea* and *Plantaginetea*, moisture in *Artemisietea* and *Galio-Urticetea*, soil reaction in *Chenopodietea*, and nutrients in *Galio-Urticetea*, *Chenopodietea* and *Plantaginetea* (Fig. 5).

Discussion

Between-habitat differences in urban vegetation

Our study indicated remarkable differences between vegetation stands attributable to different phytosociological classes, which did not change over the study period (Fig. 3). Particular classes roughly correspond to successional stages (Pyšek 1977): annual *Chenopodietea* to initial or early successional stages and perennial *Artemisieta* and *Galio-Urticetea* to later stages. *Plantaginetea* and *Agropyretea* include stands where limited successional changes take place due to frequent distur-

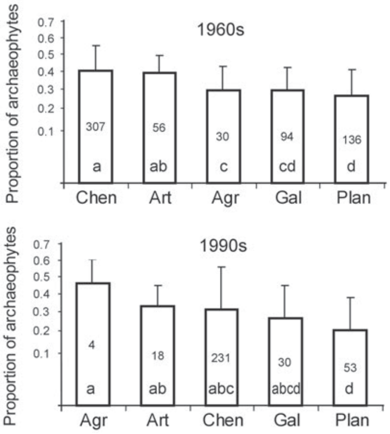

Fig. 4. Differences among mean values (with standard deviation) of phytosociological classes for proportion of archaeophytes in the 1960s and 1990s. Otherwise as in Fig. 3.

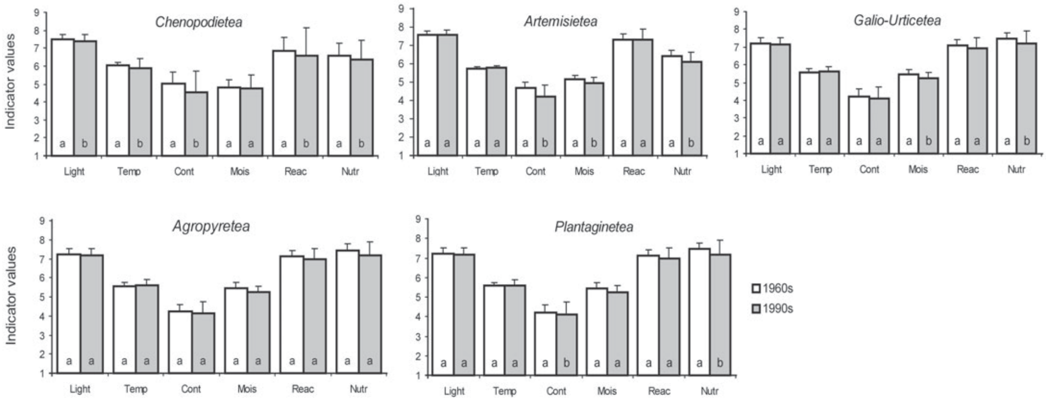

Fig. 5. Differences between mean values (with standard deviation) of the 1960s and 1990s in Ellenberg indicator values. Indicator values are light, temperature (temp), continentality (cont), moisture (mois), soil reaction (reac) and nutrients (nutr). Different letters inside the bars indicate significant differences ($P < 0.05$) between periods in one-way ANOVAs. Sample sizes as in Fig. 2.

bances; these classes have a lower species richness, lower proportion of neophytes, and (*Plantaginetea*) a lower proportion of archaeophytes. The initial or early successional vegetation of *Chenopodietea*, on the other hand, harboured more neophytes than the other classes. This agrees with studies on succession in man-made habitats where native species gradually replace aliens (Pyšek & Pyšek 1991; Meiners et al. 2002). *Chenopodietea* also had a lower evenness than the late-successional types of perennial vegetation, indicating a remarkable role of monodominant stands in early successional stages and subsequent development towards stands with a more equal distribution of species abundances.

Habitat changes between the 1960s and 1990s

The analysis of indicator values (Fig. 5) indicated that the habitats of urban synanthropic vegetation changed since the 1960s, probably largely because of increased urbanization. Increasing drought in *Artemisietea* and *Galio-Urticetea* habitats is probably associated with road and pavement construction, and land drainage for the purpose of building activities. Decreased amount of nutrients, detected in almost all vegetation types, may be partly associated with the decrease in moisture, which limits the nutrient uptake (Fitter 1986). However, urbanization may also play an important role, as some ruderal habitats such as garbage holes, dumps and rubbish tips became strongly reduced and were often replaced by buildings, parks or urban greenery. Decrease in soil reaction in disturbed habitats of *Chenopodietea* can be explained by increased speed of building construction in the 1990s compared to the past. Moreover, construction sites are nowadays restored immediately after the building is finished, which also contributes to the lower amount of calcium released into the environment. Also, there is a trend to use less salt for winter treatment of roads.

Changes in richness and proportion of alien species

We present evidence that, simultaneously with habitat changes, species richness at the scale of vegetation plots decreased over the last three decades. The decrease in the total number of species in *Artemisietea*, *Chenopodietea* and *Plantaginetea* over three decades was associated with the retreat of archaeophytes (Fig. 2). Obviously, the increasing urbanization had a strong effect upon this group of species, many of which are confined to specific habitats and are typical of village settlements rather than urban landscape (Kowarik 1995). While the significant increase in the proportional representation of archaeophytes, found only in the Agropyretea, is probably attributable to the small sample size from the 1990s – rather than reflecting a real increase – the retreat of archaeophytes seems to be a general phenomenon. This has been pointed out for Central European cities, villages and arable land (e.g. Sukopp & Werner 1983; Lososová 2003; Lososová et al. 2004). Some species of this group appear on national Red Lists of threatened taxa (Holub & Procházka 2000).

Unlike the proportion of archaeophytes, the proportion of neophytes in urban synanthropic vegetation did not change over time. This conclusion is different from that based on comparison of the entire flora of Plzeň between 1960s and 1990s (Chocholoušková & Pyšek 2003), which indicated an increase in the proportion of neophytes from 13.2% to 19.0%. The fact that their mean number and proportion in vegetation relevés did not increase over the study period indicates that most neophytes do not successfully enter the established vegetation and occur casually (Kubát & Jehlík 2003; Pyšek et al. 2004), or their distribution remains localized. They are therefore recorded in total species lists but being less abundant than native species (Crawley et al. 1996), they are rarely recorded in small-sized sample plots.

Small-scale diversity loss and large-scale homogenization

The fact that over three decades species richness of urban synanthropic vegetation decreased at the scale of vegetation plots, mostly due to retreat of archaeophytes, may indicate the process of biotic homogenization occurring at a larger scale (McKinney & Lockwood 1999; Olden et al. 2004). The decrease of ecologically specialized species such as archaeophytes and increasing predominance of generalist species in urban vegetation has been repeatedly noted in the literature, e.g. in a phytosociological context where several vegetation types could not be characterized with character species (Kopecký & Hejný 1978; Sukopp & Werner 1983; Pyšek 1991). Gradual impoverishment of ruderal vegetation has been also reported for village settlements (Brandes 1981). Thus ruderal vegetation becomes increasingly uniform, and we hypothesize that this homogenization mainly results from increasing urbanization of city areas, changes in life style and associated loss of specific habitats (Sukopp & Werner 1983).

Supporting evidence for homogenization comes from a study of the flora of Plzeň which compared species lists from three periods covering the last 120 years (Chocholoušková & Pyšek 2003) and which demonstrated that changes in species composition of urban flora are associated with a decrease in species abundances. Rare species are becoming more rare, hence they are less present in vegetation relevés. This explains a seeming contradiction between the results of the present paper, focused on plant communities, and studies comparing diversity of flora in Central European cities (Klotz 1987; Landolt 2000). In these cities, species numbers over the past 1-2 centuries remained at comparable level but approximately 30-40% of their original flora were replaced, mostly by aliens, and many of the native species that survived were restricted in their abundance. The remarkable spatio-temporal dynamics of urban vegetation, however, cannot adequately be described by comparing whole species lists for a given city in different periods (Klotz 1987; Landolt 2000; Chocholoušková & Pyšek 2003). A vegetation study, based on repeated sampling of phytosociological relevés, provides an opportunity to analyze specific trends occurring at smaller spatial scales.

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References

Bancroft, T.A. 1964. Analysis and inference for incompletely specified models involving the use of preliminary test(s) of significance. *Biometrics* 20: 427-442.

Box, G.E.P. & Cox, D.R. 1982. An analysis of transformations revisited. *J. Am. Stat. Assoc.* 77: 209-210.

Brandes, D. 1981. Gefährdete Ruderalgesellschaften in Niedersachsen und Möglichkeiten zu ihrer Erhaltung. *Gött. Flor. Rundbr.* 14: 90-98.

Chocholoušková, Z. & Pyšek, P. 2003. Changes in composition and structure of urban flora over 150 years: a case study of the city of Plzeň. *Flo*ra 198: 366-376.

Chytrý, M. 2001. Phytosociological data give biased estimates of species richness. *J. Veg. Sci.* 12: 439-444.

Chytrý, M. & Rafajová, M. 2003. Czech National Phytosociological Database: basic statistics of the available vegetation-plot data. *Preslia* 75: 1-15.

Chytrý, M., Tichý, L., Holt, J. & Botta-Dukát, J. 2002. Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13: 79-90.

Crawley, M.J. 1993. *GLIM for ecologists*. Blackwell Scientific Publications, London, UK.

Crawley, M.J., Harvey, P.H. & Purvis, A. 1996. Comparative ecology of the native and alien floras of the British Isles. *Biol. Trans. R. Soc.* B 351: 1251-1259.

Ehrendorfer, F. (ed.) 1973. *Liste der Gefäßpflanzen Mitteleuropas*. 2nd ed. Gustav Fischer Verlag, Stuttgart, DE.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Weber, W. & Paulißen, D. 1991. Zeigerwerte von Pflanzen in Mitteleuropa. *Scr. Geobot.* 18: 1-284.

Fitter, A. 1986. Acquisition and utilization of resources. In: Crawley, M.J. (ed.*) Plant ecology*, pp. 375-405. Blackwell Scientific Publications, London, UK.

Gilbert, O.L. 1989. *Ecology of urban environment*. Chapman & Hall, London, UK.

Haeupler, H. 1974. Statistische Auswertung von Punktrasterkarten der Gefässpflanzenflora Süd-Niedersachsens. *Scr. Geobot.* 8: 1-141.

Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *J. Veg. Sci.* 12: 589-591.

Holub, J. & Procházka, F. 2000. Red List of vascular plants of the Czech Republic – 2000. *Preslia* 72: 187-230.

Klotz, S. 1987. Floristische und vegetationskundliche Untersuchungen in Städten der DDR. *Düsseldorfer Geobot. Kolloq.* 4: 61-69.

Klotz, S. 1990. Species/area and species/inhabitants relations in European cities. In: Sukopp, H., Hejný, S. & Kowarik, I. (eds.*) Urban ecology*, pp. 99-104. SPB Academic Publ., The Hague, NL.

Klotz, S. & Gutte, P. 1992. Biologisch-ökologische Daten zur Flora von Leipzig – ein Vergleich. *Acta Acad. Sci.* 1: 94-97.

Kopecký, K. 1980-1984. Die Ruderalpflanzengesellschaften im südwestlichen Teil von Praha (1) - (6). *Preslia* 52: 241-267; 53: 121-145; 54: 67-89; 54:123-139; 55: 289-298; 56: 55-72.

Kopecký, K. & Hejný, S. 1978. Die Anwendung einer deduktiven Methode syntaxonomischer Klassifikation bei der Bearbeitung der strassenbegleitenden Pflanzengesellschaften Nordostböhmens. *Vegetatio* 36: 43-51.

Kowarik, I. 1988. Zum menschlichen Einfluss auf Flora und Vegetation. Theoretische Konzepte und ein Quantifizierungsansatz am Beispiel von Berlin (West). *Landschaftsentw. Umweltforsch.* 56: 1-280.

Kowarik, I. 1995. On the role of alien species in urban flora and vegetation. In: Pyšek, P., Prach, K., Rejmánek, M. & Wade, M. (eds.*) Plant invasions: general aspects and special problems*, pp. 85-103. SPB Academic Publishing, Amsterdam, NL.

Kubát, K. & Jehlík, V. 2003. *Persicaria pensylvanica* in der Tschechischen Republik. *Preslia* 75: 183-188.

Kühn, I., Brandl, R. & Klotz, S. 2004. The flora of German cities is naturally species rich. *Evol. Ecol. Res.* 6: 749-764.

Landolt, E. 2000. Some results of a floristic inventory within the city of Zürich (1984-1988). *Preslia* 72: 441-445.

Lososová, Z. 2003. Estimating past distribution of vanishing weed vegetation in South Moravia. *Preslia* 75: 71-79.

Lososová, Z., Chytrý, M., Cimalová, S., Kropáč, Z., Otýpková, Z., Pyšek, P. & Tichý, L. 2004. Weed vegetation of arable land in Central Europe: gradients in diversity and species composition. *J. Veg. Sci.* 15: 415-422.

Magurran, A.E. 1988. *Ecological diversity and its measurement*. Croom Helm, London, UK.

McCune, B. & Mefford, M.J. 1999. *PC-ORD. Multivariate analysis of ecological data. Version 4.* MjM Software Design, Gleneden Beach, OR, US.

McKinney, M.L. & Lockwood, J. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* 14: 450-453.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. 2002. Exotic plant invasions over 40 years of old field succession: community patterns and associations. *Ecography* 25: 215-223.

Moravec, J., Balátová-Tuláčková, E., Blažková, D., Hadač, E., Hejný, S., Husák, S., Jeník, J., Kolbek, J., Krahulec, F., Kropač, Z., Neuhäusl, R., Rybníček, K., Řehořek, V. & Vicherek, J. 1995. Rostlinná společenstva České republiky a jejich ohrožení (Red list of plant communities of the Czech Republic and their endangerment). 2nd ed. *Severočes Přír.*, suppl. 1995: 1-206.

Nesvadbová, J. & Sofron, J. (eds.) 1997. *Flóra a vegetace města Plzně [Flora and vegetation of the city of Plzeň*]. Západočeské muzeum, Plzeň, CZ.

Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E. & Fausch, K.D. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol. Evol.* 19: 18-24.

Prach, K., Pyšek, P. & Šmilauer, P. 1997. Changes in species traits during succession: a search for pattern. *Oikos* 79: 201-205.

Pyšek, A. 1974. Kurzgefasste Übersicht der Ruderalvegetation von der Ruderalvegetation von Plzeň und seiner nahen Umgebung. *Folia Mus. Rer. Natur. Bohem. Occid. Ser. Bot.* 4: 1-41.

Pyšek, A. 1977. Sukzession der Ruderalpflanzengesellschaften von Gross-Plzeň. *Preslia* 49: 161-179.

Pyšek, A. 1978. *Ruderální vegetace Velké Plzně [Ruderal vegetation of the Plzeň agglomeration*]. Thesis, Botanical Institute, Czechoslovak Academy of Sciences, Průhonice, CZ.

Pyšek, A. & Pyšek, P. 1988. Ruderální flóra Plzně [Ruderal flora of Pilsen]. *Sborn. Západočes. Muz. Plzeň, Ser. Nat.* 68: 1-34.

Pyšek, P. 1991. Die Siedlungsvegetation des Böhmischen Karsts. 1. Syntaxonomie. *Folia Geobot. Phytotax.* 26: 225-262.

Pyšek, P. 1993. Factors affecting the diversity of flora and vegetation in central European settlements. *Vegetatio* 106: 89-100.

Pyšek, P. 1998. Alien and native species in Central European urban floras: a quantitative comparison. *J. Biogeogr.* 25: 155-163.

Pyšek, P. & Pyšek, A. 1991. Succession in urban habitats: an analysis of phytosociological data. *Preslia* 63: 125-128.

Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G., Williamson, M. & Kirschner, J. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53: 131-143.

Pyšek, P., Sádlo, J. & Mandák, B. 2002. Catalogue of alien plants of the Czech Republic. *Preslia* 74: 97-186.

Salisbury, E.J. 1943. The flora of bombed areas. *Nature* 151: 462-466.

Sokal, R. & Rohlf, F. J. 1995. *Biometry*. 3rd ed. Freeman, New York, NY, US.

Sukopp, H. 2002. On the early history of urban ecology in Europe. *Preslia* 74: 373-393.

Sukopp, H. & Werner, P. 1983. Urban environment and vegetation. In: Holzner, W., Werger, M.J.A. & Ikusima, I. (eds.*) Man's impact on vegetation*, pp. 247-260. Dr. W. Junk Publ., The Hague, NL.

Sýkora, K.V., Kalwij, J.M. & Keizer, P.-J. 2002. Phytosociological and floristic evaluation of a 15-year ecological management of roadside verges in the Netherlands. *Preslia* 74: 421-436.

Tichý, L. 2002. JUICE, software for vegetation classification. *J. Veg. Sci.* 13: 451-453.

Vesecký, A. (ed.) 1961. *Podnebí Československé socialistické republiky. Tabulky [Climate of the Czechoslovak Socialist Republic. Tables].* Hydrometeorologký ústav, Praha, CZ.

Westhoff, V. & van der Maarel, E. 1978. The Braun-Blanquet approach. In: Whittaker, R.H. (ed.*) Classification of plant communiti*es, pp. 287-399. Dr. W. Junk , The Hague, NL.

Wiegleb, G. 1986. Grenzen und Möglichkeiten der Datenanalyse in der Pflanzensoziologie. *Tuexenia* 6: 365-377.

Wittig, R. 2002. *Siedlungsvegetation*. Eugen Ulmer, Stuttgart, DE.

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