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Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzeň

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Summary

Floristic lists of the industrial city of Plzeň, W Bohemia, Czech Republic, were compiled for the periods 1880–1910, 1960s and 1990s. Data were obtained for the city and its surroundings and abundance of each species was estimated from primary literature and recent field research. Changes in species richness on the time scale of 120 years were described, and dynamics of representation of alien species was analysed. Total number of species recorded decreased from 1173 in 1880–1910 to 988 in 1960s to 1043 in 1990s. These dynamics differed between city and surroundings. In the city, species number was gradually increasing while the trend was opposite in the surroundings. When expressed per log area, initial pattern of higher species richness in the surroundings was reversed in the course of the study period. The floristic similarity between 1880–1910 and 1990s was 0.57 for the surroundings and 0.41 for the city. In the 120 years covered, 805 species remained permanently present, 368 disappeared and 238 immigrated as new. Proportional representation of common species decreased and that of rare species increased. The representation of neophytes in the total flora of the study area increased from 6.2% in 1880–1910 to 13.2% in 1960s to 17.0% in 1990s. The proportion of native species decreased accordingly, and that of archaeophytes was stable over the study period. The representation of woody plants increased in the city, namely among neophytes. Over the study period, there was an increase in the representation of C and CR-strategists, mainly on behalf of CSR and SR strategists. CSR and CS strategies are most typical of native flora elements, C and CR of neophytes, while R and CR are most represented among archaeophytes. No consistent temporal trends in indicator values were recorded but the flora of the city differed from that of the surroundings in higher demands for light, temperature, nitrogen and soil reaction and lower demands for moisture. The present paper demonstrates that historical data on urban floras provide a powerful tool to evaluate the effect of humans on the development of urban landscapes and their plant life.

Key words: Urban flora, historical dynamics, species diversity, life history, life strategy, alien species

Introduction

In Central Europe, human activity in the last two centuries brought about the ruderalization of landscape and creation of new human-made habitat types (Sukopp 1969, 1972; Sukopp et al. 1995; Kowarik 1990). Numerous studies have investigated the plant composition of human settlements at a variety of scales so there is a good knowledge of factors promoting species richness and structuring vegetation composition in such sites (Sukopp et al. 1990, 1995; Kowarik 1995, Pyšek 1993, 1998; Wittig 2002). Urban ecology has a long history and the field has been rapidly developing in the last decades (Sukopp 2002). Studies are available describing vegetation composition of urban habitats (e.g. Kunick 1974; Pyšek 1978; Gödde 1986; Kopecký 1980–1984; see Wittig 2002 for review of available data), including successional trends (Pyšek 1977, 1978; Prach et al. 1993, 1997, 2001).

Research in urban habitats was coined by floristic studies, as these sites proved to be remarkably rich in species due to habitat diversity (Gilbert 1989) and

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enrinchment by invasions of alien species (Pyšek et al. 1998). Complete species lists were produced for a number of European cities in the second half of the 20th century (see Pyšek 1993 and references therein). Such data, although rather variable in terms of quality and the duration for which they were collated, served as a background for studies attempting to generalize the pattern of species richness and factors affecting this characteristic (Pyšek 1989, 1993; Brandes & Zacharias 1990; Klotz 1990).

Like in other fields of ecology dealing with diversity, historical data represent a unique challenge. This is particularly relevant to urban habitats where the effect of humans on composition and structure of flora is profound. Knowing about the site past history makes it possible to evaluate the influence exerted by humans on shaping local floras. Since on the time scale of centuries this influence increased remarkably, changes in flora can be attributed with a reasonable degree of certainty to the dynamics of human activities. Such data are rather rare; comparison of historical data with present situation was made for the flora of Leipzig (1867 vs. 1989, Klotz & Gutte 1992), Halle (1848 vs. 1983, Klotz 1987) and Zürich (1839 vs. 1998, Landolt 2000).

Plzeň represents another industrial Central-European city for which it was possible to extract historical data and compare them with modern records. Compared to previous studies on other cities, this data set is more detailed in that (i) the flora was comprehensively recorded in three subsequent periods, and (ii) the information available on localities of particular species made it possible to distinguish between the city and its surroundings for each of the study periods. Our study was aimed at (a) describing the changes in species richness on the time scale of 120 years, (ii) analyzing the dynamics of representation of alien species and the role they play in overall floristic richness of the city, and (iii) evaluating the importance of species life histories and life strategies as well as their ecological demands.

Study area

Plzeň (49°45′ N, 13°23′ E), an industrial center of the western part of the Czech Republic, is located at the confluence of four rivers at the altitude of 310–380 a.s.l. (for surroundings the range is 293–452 m). Mean annual temperature is 6.4–9.1 °C, annual sum of precipitation is 524 mm (Veseckÿ et al. 1958, 50-year average). The number of inhabitants increased from 86,368 at the beginning of the 20th century to 148,021 in 1960s to 165,259 in 1990s.

From a botanical viewpoint, the city of Plzeň represents one of the most thoroughly studied cities, not only in the Czech Republic but also by Central-European standards. Research on flora of the region has a long history, starting on the turn of the 19th and 20th centuries (Hora 1883; Hanuš 1885–1886; Maloch 1913). Another extensive floristic data set is available from the 1960s (Hadač et al. 1968) and the research has continued up to the recent times. Modern synthetic papers were published, including overviews of vegetation and flora in both ruderal habitats and seminatural sites in the surroundings of the city (Pyšek 1974, 1978; Pyšek & Pyšek 1988; Nesvadbová & Sofron 1997). Since most historical sources cover the present territory of the city and give reasonably precise location of particular species, it was possible to collate data on the historical development of the flora.

Data sources and methods

We distinguished three periods and for each we compiled a list of species recorded at the territory corresponding to the present city limits and settlements in its closer surroundings.

1. Several papers cover the late 19th century, with earliest records from 1880 (Hora 1883; Hanuš 1885–1886; Polívka 1901; Maloch 1913). Although some more recent works give also records from this period (Mikyška 1944a, b), research continuity of this period was completed by the flora of the region published by Maloch (1913). This period is further referred to as 1880–1910.

2. For 1960s, a regional flora of Hadač et al. (1968), covering wider surroundings of the city, was used together with the urban flora of Plzeň (Pyšek & Pyšek 1988), which contains dated information from 1960s. For this period, unpublished floristic records of Antonín Pyšek were also used.

3. For 1990s, a synthetic floral work covering both the city and its surroundings was used as a data source (Nesvadbová & Sofron 1997). The information was completed by using specialized floristic papers (Kupecká 1998; Horková 2001) and field research of the first author of the present paper conducted in 1996–2001 (see Chocholousková & Pyšek 2003).

The study territory was divided into the city of Plzeň and its close surroundings (further termed zones). The city was delimited according to the present situation and included the following city parts: Křimice, Radčice, Bolevec, Bukovec, Újezd, Doubravka, Lobzy, Božkov, Koterov, Černice, Radobyčice, Litice, Valcha, Nová Hospoda (total area 124.8 km^2). Surroundings included cadastral area of settlements in the closer neighbourhood of the city: Zbůch, Dobřany, Nezvěstice, Rokycany, Holoubkov, Březina, Nadryby, Horní Bříza, Ledce, Chotíkov, Kozolupy, Nýřany (total area 809.4 km^2).

For each period and zone, a complete list of vascular plant species was compiled by using information on localities of particular species in primary sources. The nomenclature of taxa was unified according to the recent Key to the flora of the Czech Republic (Kubát et al. 2002). Obviously erroneous past records and doubtful species, i.e. those taxonomic status of which is nowadays considered uncertain, were excluded, especially from the earlier lists. Hybrids were also excluded, except of those that are common and easily recognizable. Cultivated species were not considered. If a species was only planted in the past and started to escape from cultivation in one of the later periods, it was only counted for the period of spontaneous occurrence.

As the data sources contained information on species abundance, a three-degree scale was used to characterize how abundant a species was in the three periods and zones studied. We distinguished rare (scored 1), scattered (2) and common species (3). The former two categories are explicitely mentioned in the sources used to create the species list from the period 1880–1910 (HORA 1883; HANUŠ 1885–1886). In 1960s and 1990s, systematic research was carried out (PYŠEK & PYŠEK 1988; NESVADBOVÁ & SOFRON 1997; CHOCHOLOUŠKOVÁ & PYŠEK 2003) which made it possible to express the frequency of the majority of species. Those that occurred up to 2.0% of the total number of localities were considered rare, those in 2.1–25.0% localities as scattered and other species as common. The nature of the data did not make it possible to use a more detailed classification of common species that could be related to the 1880–1910 period. For some species in some periods, no data on abundance were given; these species were excluded from analyses taking abundance into account.

Species were characterized by their immigration status (HOLUB & JIRÁSEK 1967; RICHARDSON et al. 2000). Archaeophytes (introduced to the territory of the Czech Republic before the year 1500), neophytes (introduced after that date) and native species were distinguished. The classification followed the recently published catalogue of alien plants of the Czech Republic (PYŠEK et al. 2002). Other characteristics used were life history and life strategy. We distinguished several broad life history categories, i.e. (i) annuals and biennials, (ii) perennials, (iii) shrubs, and (iv) trees (data taken from KUBÁT et al. 2002). Grime's scheme of life strategies was used (GRIME 1979); the data on particular species were obtained from GRIME et al. (1988) and FRANK & KLOTZ (1990). The following Ellenberg indicator values were taken from FRANK & KLOTZ (1990) to characterize the ecological conditions of habitats: light, temperature, moisture, soil reaction and nitrogen.

Statistical analysis was carried out using G-test on contingency tables. Complex contingency tables were tested following CRAWLEY (1993, p. 255–261). Differences in indicator values were tested using fixed-effect one- or two-way ANOVA. The adequacy of the fitted models was confirmed by plotting standardized residuals against fitted values, and by normal probability plots of the fitted values (CRAWLEY 1993). Statistically significant differences between means for particular periods (1880–1910, 1960s, 1990s) were compared using LSD test (SOKAL & ROHLF 1995).

Results

Species numbers and pattern of floristic similarity in space and time

Total number of species recorded at the territory of Plzeň and its surroundings decreased from 1173 recorded in 1880–1910 to 988 in the 1960s and then slightly increased to 1043 in 1990s (Fig. 1). Over the whole span of the study, this represents a decrease by 11.1% during ca. 120 years. Total number of taxa recorded during the whole study period was 1459.

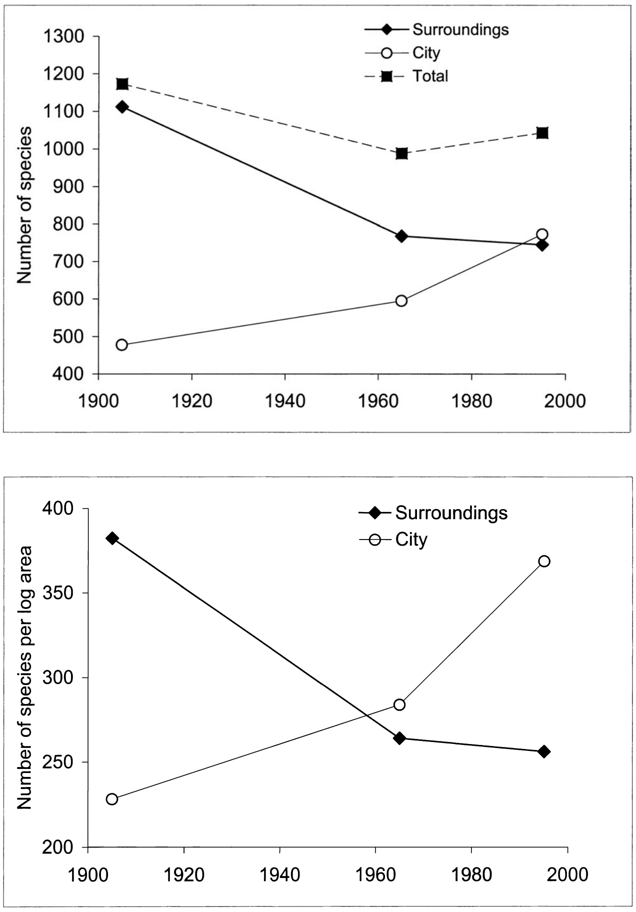

Fig. 1. Historical changes in floristic richness at the study territory. Changes in species numbers are shown separately for the city of Plzeň and its surroundings. Data points are located in the middle of study periods. (a) Species numbers. (b) Species numbers per log area.

Table 1. Abundance of species recorded at the territory of Plzeň and its surroundings in particular study periods. See text for inferring the categories of abundance from original sources. No data = species for which the estimate of abundance was missing from original sources. G-test on complex contingency tables revealed a significant effect of the abundance × period (χ^2 = 365.3, df 4, P < 0.01), abundance × zone (χ^2 = 124.1, df 2, P < 0.01) and period × zone interactions (χ^2 = 114.9, df 2, P < 0.01).

Abundance	Surroundings			City		
	1880–1910	1960s	1990s	1880–1910	1960s	1990s
Rare	411	221	241	119	402	489
Scattered	203	221	197	58	144	207
Common	471	228	181	286	35	36
No data	27	98	126	15	14	41
Total	1112	768	745	478	595	773

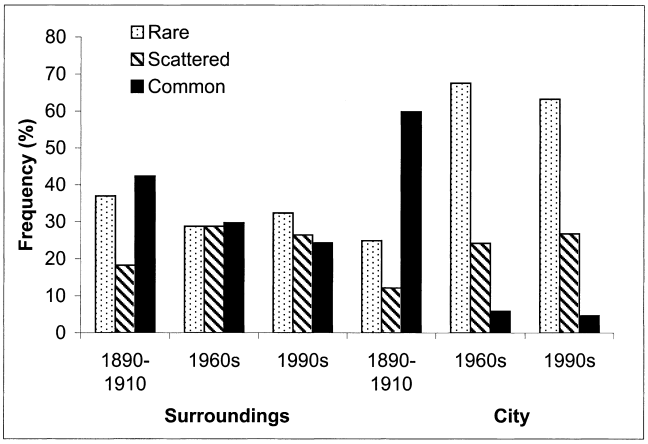

Fig. 2. Changes in the relative abundance of plant species growing at the territory of Plzeň and its surroundings in the last 120 years. Only species for which the abundance could have been estimated from original sources are shown (see Table 1). Differences in representation of particular categories of abundance were significant both for the surroundings and the city (see Table 1 for statistical analysis).

The historical pattern of floristic diversity differed between the city and surroundings (Fig. 1a). In the city, species number was gradually increasing (from 478 to 595 to 773 in particular study periods) while the trend was opposite in the surroundings (from 1112 to 768 to 745). This contrasting pattern is even more obvious when species numbers are expressed per log area to control for different sizes of zones. Using this measure, surroundings were much richer in species in 1880–1910. In 1960s the values were similar for both zones but in the following three decades, the pattern of species richness was reversed. In 1990s, the city exhibited a higher floristic diversity than surroundings (Fig. 1b).

Floristic similarity between the city and its surroundings, expressed as JACCARD coefficient, gradually increased from 0.35 in 1880–1910 to 0.38 in 1960s to 0.46 in 1990s. It also increased over time both in the surroundings (from 0.60 between 1880–1910 and 1960s to 0.65 between 1960s and 1990s) and in the city (from 0.45 to 0.58, respectively). In the study period, the surroundings have changed less than the city in terms of floristic similarity. The JACCARD coefficient between 1880–1910 and 1990s was 0.57 for the surroundings and 0.41 for the city. Changes in floristic similarity of the total flora followed a pattern similar to that found in separate parts of the city: it increased over time from 0.62 between 1880–1910 and 1960s to 0.69 between 1960s and 1990s. In the 120 years covered, 805 species were permanently present, 368 species present in the 19th century disappeared and 238 species which were not recorded in the first period immigrated into the study area. This gives the value of JACCARD coefficient 0.57 and indicates 43% turnover in species numbers.

The changes concerned not only species numbers but also their abundance. The distribution of species abundances was significantly affected by zone, period and their interaction (Table 1). On an historical time scale, proportional representation of common species decreased and that of rare species increased (Fig. 2). This trend was most obvious in the city, especially if the situation in 1880–1910 is compared with present. However, the number of rare species in the surroundings of the city increased on behalf of scattered and common species also in the second half of the 20th century, i.e. between 1960s and 1990s. Within this period, the number of common species in the city remained the same and the decrease in the proportional representation of this category is due to the increase in the number of rare species (Table 1, Fig. 2).

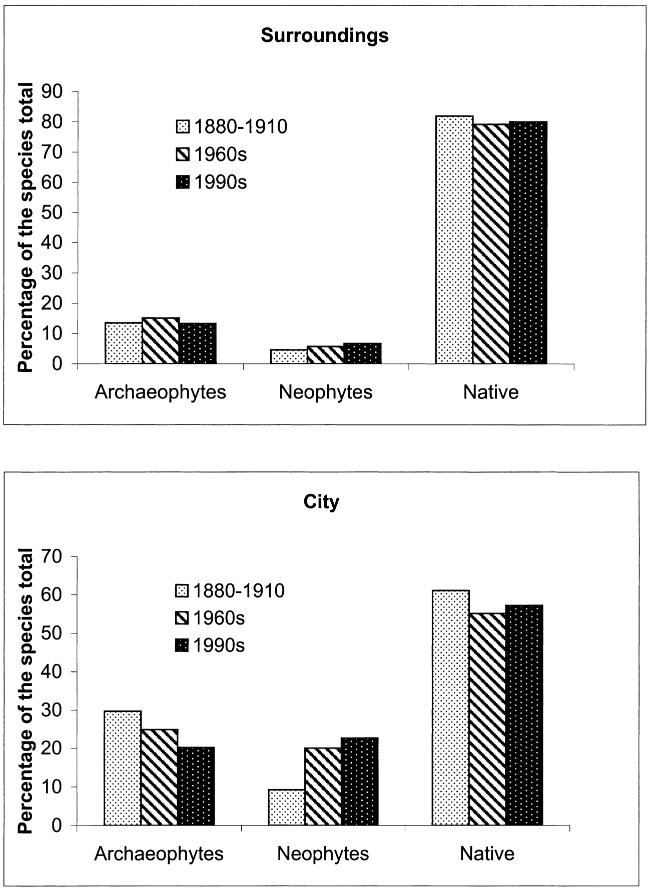

Fig. 3. Changes in the proportional representation of immigration status groups shown separately for (a) surroundings of Plzeň, and (b) the city. The differences were significant for the city ($\chi^2 = 47.60$, df 4, $P < 0.01$) but not for the surroundings ($\chi^2 = 5.26$, df 4, $P < 0.01$).

Representation of alien species

Among 1459 species recorded in all three study periods, there were 198 archaeophytes (13.6%), 225 neophytes (15.4%) and 1036 native species (71.0%). The representation of neophytes in the total flora of the study area increased from 6.2% in 1880–1910 (73 species) to 13.2% in 1960s (130 species) to 17.0% (177 species) in 1990s. The proportion of native species decreased from 79.2% in 1880–1910 (929 species) to 70.3% in 1960s (695 species) to 67.7% (706 species) in 1990s. Representation of archaeophytes was rather stable over the study period: 14.6% in 1880–1910 (171 species), 16.5% in 1960s (163 species) and 15.3% (160 species) in 1990s.

However, the pattern over time differed remarkably between the zones. While no changes in the immigration status occurred in the city surroundings over the 120 years (Fig. 3a), there was a steady increase in the proportion of neophytes, and at the same time, a decrease in that of archaeophytes and native species in the city (Fig. 3b). The shift in representation of the three groups in the total flora was thus caused by changes in the city.

Because of possibly different evaluation of abundance in the first study period, only comparison of 1960s with 1990s was carried out. Mean abundance values indicate that no substantial changes occurred during these three decades. In the surroundings, the values for both periods were 2.0 ± 1.5 and 1.7 ± 1.4 for archaeophytes and 1.7 ± 1.4 and 1.8 ± 1.6, respectively, for neophytes. Corresponding values in the city were 1.6 ± 0.8 and 1.5 ± 0.8 for archaeophytes and 1.3 ± 0.6 and 1.2 ± 0.7, respectively, for neophytes.

Changes in species traits and ecological demands

Life histories

In the total flora recorded over the whole study period, there were 872 perennials (59.8%), 412 annuals or biennials (28.2%), 123 shrubs (8.4%) and 52 trees (3.6%). There was a significant effect of period, zone and their interaction on the distribution of life histories (Table 2). The city had more annuals and less perennials, and representation of woody plants, both shrubs and trees, increased over time in this zone (Table 2). By 1990s, their representation reached 280% of the 19th century state. Their increase was also quite remarkable in terms of species numbers, from 26 in 1880–1910 to 51 in 1960s to 117 in 1990s. Unlike in the city, the increased representation of woody species in the surroundings was due to the decrease in the number of perennial species, making the proportional representation of other life history groups higher. The numbers of species in the surroundings did not change consistently for either shrubs (76, 57, 66) or trees (28, 24, 33).

The increase in representation of woody species was most remarkable in neophytes in the city; they contributed 4.5% to the total number of species in 1880–1910 (all of them were shrubs at that time), 6.7% in 1960s (4.2% shrubs, 2.5% trees) and 18.9% in 1990s (12.0% shrubs, 6.9% trees). The number of neophyte woody species in the city increased from 2 to 8 to 33 over the study period.

Life strategies

Information on life strategy was available for 1305 species, i.e. 89.4% of the total recorded in all three periods. Among them, CSR (28.2%) and C (27.9%) strategists were most represented, followed by CS (14.0%), CR (13.5%), R (8.6%), SR (5.9%) and S (1.9%) strategy. Over time, there was a slight increase in the representation of C and CR-strategists, mainly on behalf of CSR and SR strategists, and the representations of strategies was significantly different between periods (Fig. 4a). In the city, a proportional increase of C-strategy plants was more profound than in the surroundings, starting with 22.8% in 1880–1910 and reaching 30.5% in 1960s and 35.4% in 1990s. Retreat of SR-strategists was consistent in both parts of the city, i.e. surroundings (6.7 to 5.5 to 3.8%) and center (7.5 to 4.5 to 4.5%).

Table 2. Representation of life histories in particular periods and city zones. Percentage of the total species numbers are shown. G-test on complex contingency tables revealed a significant effect of the life form × period (χ^2 =19.2, df 2, $P < 0.01$), life form × zone (χ^2 = 22.9, df 2, $P < 0.01$) and period × zone interactions (χ^2 = 151.6, df 2, $P < 0.01$). Distribution of life forms was significantly different also for total flora (χ^2 = 19.6, df 6, $P < 0.01$). In statistical analysis, shrubs and trees were considered as separate categories.

	Surroundings			City			Total flora		
Life history	1880–1910	1960s	1990s	1880–1910	1960s	1990s	1880–1910	1960s	1990s
Annual, biennials	24.9	24.1	20.6	41.6	37.0	32.2	26.9	28.6	26.3
Perennial	65.7	65.4	66.1	52.9	54.5	52.7	64.2	61.3	59.4
Shrub	6.8	7.4	8.8	3.8	5.4	9.2	6.5	6.7	9.4
Trees	2.5	3.1	4.4	1.7	3.2	6.0	2.5	3.3	4.9
Woody plants total	9.4	10.5	13.3	5.4	8.6	15.1	9.0	10.0	14.3

The groups of immigration status highly significantly differed in their life strategy spectra. CSR and CS types are most over-represented in the native flora, C and CR in neophytes, while R and CR are most represented among archaeophytes (Fig. 4b).

Indicator values

The effect of the respective zone on the mean indicator value was always significant while that of the period was never significant. In nitrogen, there was a significant interaction of period and zone indicating the highest value in the 1960s and lower ones in both 1880–1910 and 1990s (Table 4). Plant species recorded in the city had higher mean indicator value for light, temperature, soil reaction and nitrogen but lower for soil moisture (Table 3–4). No temporal trends were found when comparing the effect of period on total flora for all indicator values (light: df 2, 2650; F = 0.22; temperature: df 2, 1778; F = 0.74; moisture: df 2, 2433; F = 1.98; reaction: 2, 1755; F = 0.90) but nitrogen (df 2, 2283; F = 4.68, P < 0.01). The total flora from 1960s had a higher nitrogen value than that from the other two periods which were not significantly different from each other.

Discussion

The nature of the data

Reconstruction of past floras on the basis of literature data is a difficult task because of variation in source reliability, research methods and approaches used. The profound effect of research intensity on reported species numbers may be demonstrated using the example of Warsaw. In this city, investigations on flora lasting several years in 1980s (Sudnik-Wójcikowska 1987, 1988) yielded 1416 species, more than double the species number of 604 obtained in 1960s by shorter and less intensive research (Pyšek 1995). This is not the case of the present study where the sampling intensity was comparable in the three periods. However, some differences are unavoidable whenever the subsequent sampling is carried out by different authors. For example, the decrease in total species numbers from the earliest period till 1960s and the subsequent increase can be partly explained ecologically by an increase of neophytes, but part of the reason must be probably sought also in the nature of the basic data. This is indicated namely by comparing the number of native species in the total study area which decreased from 929 to 695 between the first two periods and increased to 706 in 1990s. There are species which were recorded in the earliest and latest period, but not in the middle one, some of them rather rare or with special phenology so that they apparently escaped from recording in 1960s (e.g. *Carex pulicaris, Cerastium semidecandrum, Eleocharis mammilata, Lemna trisulca, Thalictrum lucidum, Veronica verna, Vicia cassubica*). Another group of species that were missing in 1960s and present in 1990s is associated with the level of taxonomic expertise, as in the case of the genus *Rubus;* there were 16 species reported both in 1880–1910 and 1960s but 21 species in 1990s. Obviously, it is difficult to find a sensible explanation of this increase other than improving floristic knowledge. These examples indicate that there was some sampling bias resulting from a lower research intensity in the

Table 3. Ellenberg indicator values (mean ± S.D.) for city surroundings, center and total flora in particular study periods. See Table 4 for statistical analysis.

Period	Factor	Surroundings	Center	Total flora
1880–1910	Light	6.7 ± 2.0	7.1 ± 2.1	6.7 ± 2.0
	Temperature	5.6 ± 1.4	5.8 ± 1.6	5.6 ± 1.4
	Moisture	5.6 ± 2.6	5.0 ± 2.3	5.6 ± 2.6
	Soil reaction	6.1 ± 2.0	6.5 ± 1.8	6.1 ± 2.0
	Nitrogen	4.7 ± 2.2	5.5 ± 2.2	4.8 ± 2.2
1960s	Light	6.7 ± 2.1	6.9 ± 2.2	6.8 ± 2.1
	Temperature	5.5 ± 1.4	5.9 ± 1.7	5.7 ± 1.5
	Moisture	5.4 ± 2.5	5.2 ± 2.2	5.4 ± 2.4
	Soil reaction	6.0 ± 2.0	6.3 ± 1.8	6.1 ± 2.0
	Nitrogen	4.8 ± 2.2	5.8 ± 2.1	5.1 ± 2.2
1990s	Light	6.6 ± 2.1	6.8 ± 2.3	6.7 ± 2.2
	Temperature	5.4 ± 1.5	5.8 ± 1.8	5.6 ± 1.6
	Moisture	5.6 ± 2.4	5.1 ± 2.2	5.4 ± 2.4
	Soil reaction	5.9 ± 2.0	6.4 ± 1.8	6.1 ± 2.0
	Nitrogen	4.9 ± 2.2	5.5 ± 2.2	5.1 ± 2.2

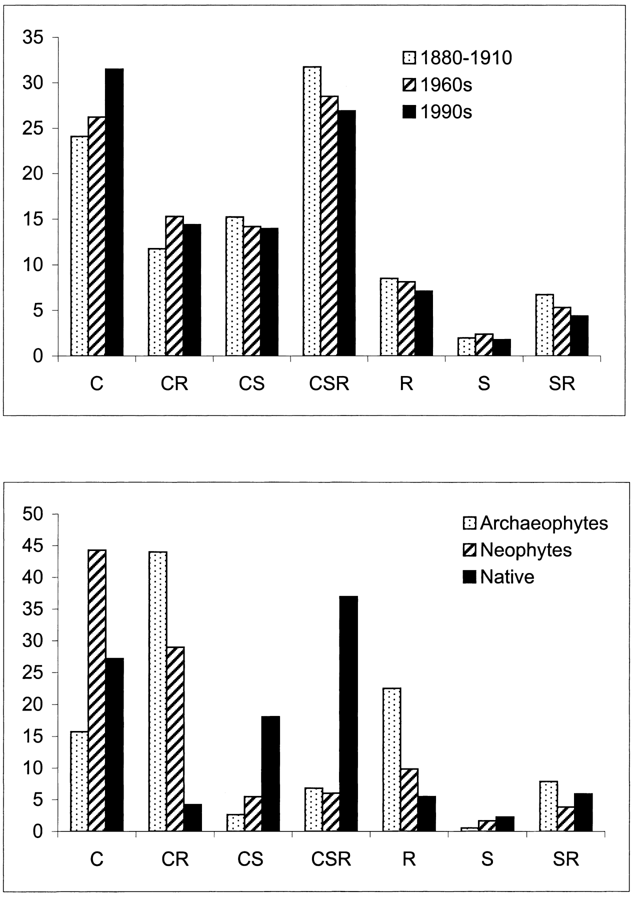

Fig. 4. Changes in the proportional representation of life strategies in (a) total flora over the study period. Differences were significant in G-test on contingency tables (χ^2 = 27.72, df 12, P < 0.01) (b) Differences in representation of life strategies of particular groups of immigration status, analyzed for the total flora recorded between 1880–1910 and 1990s. Differences were highly significant in G-test on contingency tables (χ^2 = 427.65, df 12, P < 0.01).

1960s. This must be borne in mind when interpreting the results. Nevertheless, the conclusions drawn in the present paper are based on robust patterns and seem to be valid despite this possible bias.

Historical trends in species numbers and abundance

The few quantitative data sets that are available on the historical dynamics of floristic diversity of urban sites indicate that changes may go in both directions, i.e. increase or decrease in the number of species present. However, these changes are not dramatic as the differences only account for about 10% of species numbers. In Zürich, the number of species in the city flora increased from 1104 to 1211 between 1839 and 1998 (LANDOLT 2000) and in Halle, the number of species remained relatively stable in the period 1848–1983 (KLOTZ 1987). Nevertheless, while species number that can be accomodated in a city of certain size remains relatively stable (PYŠEK 1993), the composition of the flora may change dramatically. The floristic similarity between the earliest and the most recent period of the present study was as low as 57%; in Zürich it was 66% (LANDOLT 2000). This indicates that the negative effect of humans on plant life in cities is manifested through the composition of flora and by a decrease of species abundances. It appears that in Central European cities, species numbers over the last 1–2 centuries remained at a comparable level, but approximately 30–40% of the original flora were replaced, mostly by aliens, and many of the native species that survived were restricted in their abundance.

Some clear trends were revealed in the present study, namely the pattern in species richness. These trends reflect changes in the character of the study area during

Table 4. Effect of period (1880–1910, 1960s, 1990s) and zone (city vs. surroundings) on Ellenberg indicator values tested by

Source of variation	Light[1]				Temperature[2]				Moisture[3]			
	SS	df	MS	F	SS	2	MS	F	SS	df	MS	F
Period	5.52	2	2.76	1.35 NS	1.32	1	0.66	0.61 NS	9.70	2	4.85	1.02 NS
Zone	66.39	1	66.39	32.4 ***	66.15	2	66.15	60.9 ***	161.30	1	161.30	34.1 ***
(Period) × (Zone)	4.64	2	2.32	1.13 NS	0.98	2529	0.49	0.45 NS	15.71	2	7.86	1.66 NS
Error	7798.8	3807	2.05		2744.5	2534	1.085		15261	3488	4.38	
Total	7875.3	3812			2813.0				15447	3493		

[1] Lower L value in the surroundings than in the city
[2] Lower T value in the surroundings than in the city
[3] Higher M value in the surroundings than in the city

the study period. The results reflect changes in the ruderal flora under the scenario of the development and industralization of the city and its surroundings. Species enrichment in the city was undoubtedly due to its gradual ruderalization. The delimitation of this zone in the present paper was based on the present city limits and part of this zone was therefore not built-up and less disturbed in the first period (Fig. 5). Increasing urbanization thus reflected the pattern of higher species richness in cities compared to the surrounding landscape (Haeupler 1974). The same factor acted in opposite direction in the surrounding landscape with adjacent settlements; these were also less disturbed at the beginning of the study period, harbouring therefore more species from seminatural and natural vegetation. Increasing urbanization of the landscape in the second half of the 20th century reduced the total species number by deterioration of conditions for many of these species, but their retreat was not fully compensated by an enrichment, namely in villages, due to increasing influence of humans. Compared to the city, there was virtually no increase of neophytes encroaching this zone (51 in 1880–1910 compared to 50 in 1990s) and quite a remarkable decrease of archaeophytes (150 to 99, respectively) which, similarly to native species, were increasingly limited by loss of habitats.

The comparison of the first period with the latter two reflects different aspects than the comparison of the two periods of the 20th century. However, the two recent periods can be used to infer a more subtle reflection about the response of ruderal flora to increasing human pressure because from 1960s up to now, the character of the city has not changed dramatically (Fig. 5). Most conspicuous changes in the last three decades concern the representation of particular groups of aliens (increase in neophytes and decrease in archaeophytes) and shifts in the spectra of life strategies. Continuing invasions of alien species also resulted in shifts of life history spectra; the proportion of woody species was steadily increasing as a result of increasing escapes from cultivation.

The nature of the historical data analysed in the present paper makes it possible to evaluate changes in flora by using not only temporal but also spatial information and the results document that the pattern of historical development of the flora in an industrial city and its surroundings is not uniform; in some aspects it is even contrasting. Opposite trends in the dynamics of species diversity were found for the city and its surroundings. Species numbers decreased in the latter and increased in the former zone. In the second half of the 19th century, surroundings were clearly richer in species. The time span of the study made it possible to record the gradual shift in this pattern, with the city becoming floristically more rich than its surroundings (when corrected for the different size of the areas, see Rejmánek 1996). Moreover, the information on species abundance and its changes over the study period indicates that over the last century more species became rare and an increasing proportion of species were retreating.

It must be borne in mind, that taking into account the species abundance the results must not be overestimated because of the difficulty to relate measures used by different authors and transformation of verbal description of abundance into a semiquantitative scale. This caution concerns especially the earliest study period from the turn of the 19th and 20th centuries (Hora 1883, Hanuš 1885–1886). Species abundances from this period were most difficult to relate to the two recent records from 1960s and 1990s, and it cannot be excluded that they are overestimated. However, there are two reasons supporting the observed trend regardless this caution. First, the differences in the distribution of species abundance between the first and the second two periods are so striking

two-way factorial ANOVA. NS = not significant, * P < 0.05, ** P < 0.01, *** P < 0.001

Reaction[4]				Nitrogen[5]			
SS	df	MS	F	SS	df	MS	F
2.57	2	1.29	0.34 NS	55.97	2	27.99	5.95 **
96.70	1	96.70	25.33 ***	489.30	1	489.30	103.95 ***
3.57	2	1.79	0.47 NS	18.78	2	9.39	1.99NS
9261.8	2426	3.82		15397	3271	4.71	
9364.6	2431			15961	3276		

[4] Lower R value in the surroundings than in the city
[5] N value lower in the surroundings than in the center. The value from 1880–1910 does not differ from that in 1990s but both are lower than in 1960s

abundance during 160 years, and those that increased exhibited higher demands for temperature and nutrients.

These trends are most obvious in the city, especially if the situation in 1880–1910 is compared with present. A high number of rare species is a consequence of two processes. First, introduction of a large number of propagules of alien species, many of which occur only temporarily and do not form long-persisting populations. Such species contribute to the proportional increase of representation of rare species. Second, under the increasing disturbance ruderal habitats in the city became more uniform in the course of the study period, and a low number of competitively strong dominant species prevailed, leaving less possibilities for populations of other species.

Indicator values and life strategies

Surprisingly, indicator values of the total flora of Plzeň and its surroundings did not exhibit any shift in the last 120 years, with the only exception of nitrogen. The highest value for nitrogen, found in the 1960s, might reflect that its supply has been increasing since the beginning of the 20th century but after reaching its peak, it started to decrease. A possible explanation seems to be that with increasing degree of urbanization, some ruderal places such as garbage holes, dumps and rubbish tips became strongly reduced. Non-significant results obtained on total flora for other indicator values do not necessarily mean that landscape and climate changes (e.g. acid rain) and a potential effect of global warming (increase in temperature and more drought) have no significant effects on the composition of local flora. These changes are, however, too subtle to be detected by the relatively rough measure of indicator values. The remarkable species turnover over the last 120 years (43%) would be probably better explained by other factors involved and species responses to their action, such as the overall effect of human-induced disturbance, as described by the hemeroby concept (KOWARIK 1988; KIM et al. 2000; SÝKORA et al. 2002). The species spectrum has changed remarkably but principal ecological demands of the flora remained the same.

However, there are differences in ecological conditions, reflected by indicator values, between the city and its surroundings, and these differences persisted over the whole last century. Our study confirmed previously reported differences between habitat characteristics of the urban flora and that of less disturbed areas, represented here by the surroundings of the city. Species in the city have higher demands especially for temperature and nitrogen and lower demands for moisture (WITTIG & DURWEN 1982; KLOTZ 1984; PYŠEK & PYŠEK 1990; WITTIG 2002).

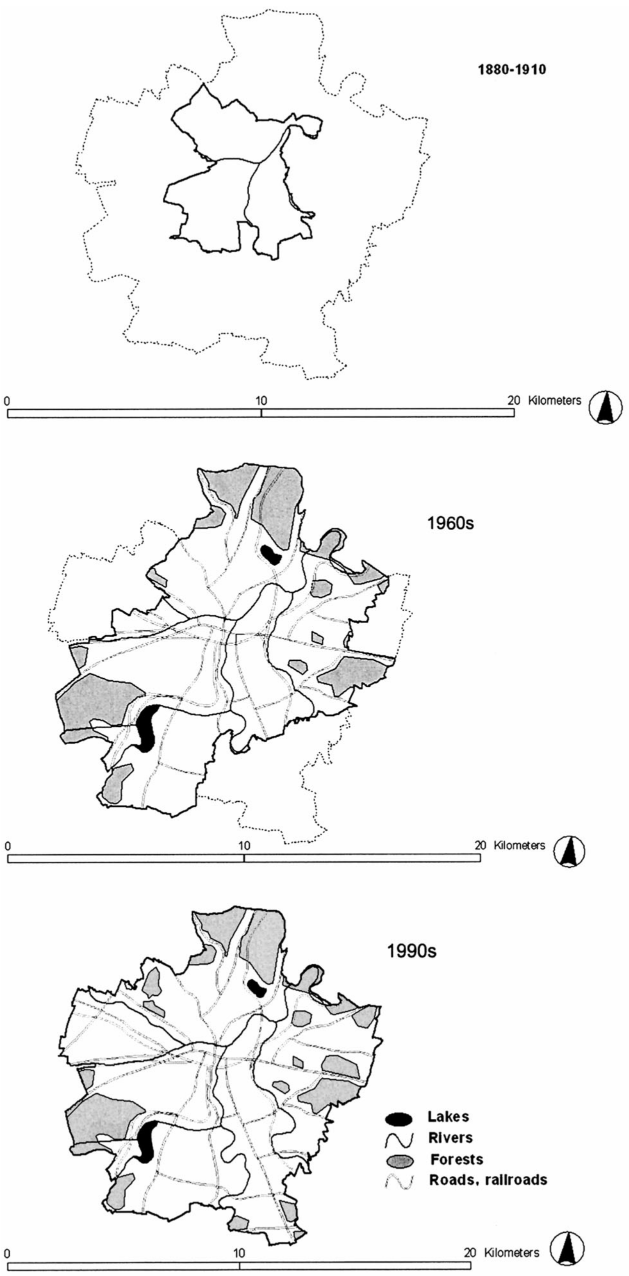

Fig. 5. Changes in the character of the city of Plzeň during the study period. City limits for each period are indicated by the shape of the map, and 1990s city limits are indicated for 1880–1910 and 1960s using a dotted line. The information on the distribution of forests and roads was not available for the first period.

that they obviously reflect the real situation. Second, the trend of more species becoming rare and less species becoming common is confirmed by comparing 1960s with 1990s. LANDOLT (2000) compared the historical and recent composition of the urban flora of Zürich and also found that more species decreased than increased in

The spectra of GRIME's life strategies analysed in the present study closely correspond to the results from Leipzig (KLOTZ & GUTTE 1992) and Halle (KLOTZ 1984). This holds not only for the proportion of particular strategies but, more importantly, also for the historical dynamics of their representation. Previous studies from the two German cities, comparable with Plzeň in terms of size and degree of industrialization, came to the same conclusion about the increase in proportional representation of C and CR strategies on behalf of CSR and other types (KLOTZ 1984; KLOTZ & GUTTE 1992). Combined strategies involving stress tolerance are retreating with increasing urbanization and disturbance (GRIME 1979), while competitively strong dominants with principal role of C strategy increased their representation in urban flora on an historical time scale.

Representation of alien species

The contribution of neophytes found in the present study can be compared to extensive data from literature. In 54 European cities the average value was 25.2%, ranging from 11 to 48% (PYŠEK 1993). The rather low value recorded for the total flora (17.0%) is due to the spatial focus of the present study which included city surroundings with less disturbed habitats and therefore a lower proportion of alien species. The majority of studies dealing with urban flora are limited to inner cities where the representation of aliens is higher (WITTIG 2002). The value obtained for the city of Plzeň in 1990s (22.6%) is well within the European average. The proportion of archaeophytes recorded in the present study (15.3%) corresponds almost exactly to the European average recorded for the 54 cities mentioned (15.2%).

While the representation of neophytes in the city was steadily increasing both in terms of species numbers and proportion, the composition of the flora in the surroundings is surprisingly stable with respect to invasions by alien species. Not only that the proportional representation of native species, archaeophytes and neophytes has not changed but reliable data on abundance in particular groups suggest that between 1960s and 1990s it has not changed either.

The present paper demonstrates that if we are aware of their limitation, historical data on urban floras provide a powerful tool to evaluate the effect of humans on the development of urban landscapes and response of flora to human-caused disturbances. Unfortunately, such data sets remain so far limited to Central Europe (KLOTZ 1984; KLOTZ & GUTTE 1992; LANDOLT 2000) and are therefore too rare to allow generalization on a wider geographical scale.

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