Journal of Biogeography (1998) **25**, 155–163

Alien and native species in Central European urban floras: a quantitative comparison

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Abstract. The paper provides quantitative information on the occurrence of alien species in Central European cities and analyses factors determining the richness of alien and native floras in this habitat type. Data for 54 cities (25 Polish, 24 German, 4 Czech and 1 Austrian) were gathered, and the representation of archaeophytes (i.e. aliens introduced before 1500 AD), neophytes (introduced after that date) and native species was expressed. In an average city there were 87.4 archaeophytes (15.2% of the city flora) and 172.4 neophytes (25.2%) giving a total of 259.7 for alien species (40.3%). The number of native species averaged 386.5. The numbers of species in each category of immigration status increased significantly with city size. For neophytes, the species-area relationship showed a higher slope (0.49) on log–log axes than for both archaeophytes (0.16) and native species (0.30). Not only the number, but also the relative contribution of neophytes to the total flora, increased with city size, indicating that neophytes are the group which are most closely associated with human activity. On the other hand, archaeophytes were better represented in smaller cities, as they were confined to rural environment. A step-wise multiple regression was used to test for environmental variables acting as significant predictors, and explained between 40 and 65% of variation in the species numbers for particular categories of immigration status, providing the best fit for neophytes. City size was the best predictor for each characteristic, except of the proportion of total aliens, where the percentage of explained variability was low (8.2%), with latitude being the only significant predictor. Temperature was another highly significant predictor for the number of archaeophytes and total aliens, reflecting the origin of aliens in warmer areas. There was an effect of region on some flora characteristics. Polish cities had significantly higher proportion of archaeophytes and of total aliens than German cities. It is concluded that the occurrence of native and alien species in urban floras follows rather different pattern.

Key words. Plant invasions, Urban flora, Central Europe, Species-area relationships, Environmental conditions, Quantitative pattern.

INTRODUCTION

The flora of human settlements has received considerable attention in the last few decades (Sukopp, 1990; Pyšek, 1995b). It has been recognized that cities harbour more species than the surrounding landscape (Walters, 1970; Haeupler, 1974; Wittig & Durwen, 1981; Kowarik, 1985; Pyšek, 1993) and that species richness is closely related to city size (Klotz, 1988, 1990; Pyšek, 1989, 1993; Brandes & Zacharias, 1990). The high diversity of urban flora is usually explained by habitat heterogeneity and the good possibilities of species immigration in big cities, where the contribution of aliens to the total number of species is remarkable (Sukopp *et al.*, 1979; Sukopp & Werner, 1983; Kowarik, 1990).

In studies on plant invasions, the focus is rather on natural habitats (Cronk & Fuller, 1995; Pyšek, 1995b). Nevertheless, understanding the behaviour of alien species in cities is of crucial importance, since the cities serve as immigration sources (Sukopp & Werner, 1983) from which the aliens can spread further into the landscape (Pyšek, 1998).

Studies evaluating the role of alien species in large urban agglomerations has mostly focused on the spatial pattern of their occurrence (Kowarik, 1990; see Pyšek, 1995c for a review), some authors have described the changes over time by comparing floristic lists compiled over the territory of a single city in different time periods (Klotz, 1987). However, floristic lists of several European towns and cities are available and their appropriate comparative analysis can reveal new and interesting information (Kunick, 1982).

Surprisingly, despite the floristic data available the generalizations on the proportion of aliens in urban floras were often simplistic without a solid quantitative background (Falinski, 1971). By bringing together scattered data from various sources, the present study thus aims at providing the basic quantitative information on the occurrence of alien species in this habitat type. By analysing relatively large data set, it attempts to answer the following questions: (i) What are the factors determining the richness of alien flora in central European cities? (ii) Do the principal factors differ from those determining the pattern in native flora occurring at the city territory?

DATA SOURCES AND METHODS

Definition of terms

The following categories were distinguished for the purpose of the present paper with respect to the species' immigration status: (1) **Native** (indigenous) species is one which evolved in the area or which arrived there by one means or another before the beginning of the neolithic period or which arrived there since that time by a method entirely independent of human activity (Webb, 1985). (2) **Alien** (introduced, exotic, adventive) species is one which reached the area as a consequence of the activities of neolithic or postneolithic man or of his domestic animals (Webb, 1985; see Pyšek, 1995a for a discussion of terminology). Aliens were further divided into two groups, following the classifications based on the time of immigration (e.g. Holub & Jirásek, 1967): (3) **archaeophytes** were introduced to Central Europe before 1500, mostly from the Mediterranean area, and they are typical weeds of arable land whereas (4) **neophytes** occur as a result of later introductions, both intentional and unintentional (including ephemerophytes in the sense of Holub & Jirásek, 1967). The escapees from the cultivation of crops and ornamental plants, though usually classified into separate group in phytogeographical studies of man-accompanying flora, were also included among the latter. Hence, in the context of the present paper, any spontaneously occurring non-native species that appeared after the discovery of America is considered a neophyte.

In studies on plant invasions, only the neophytes are usually understood as aliens because of the trend to consider long-established species, i.e. archaeophytes, as native (Webb, 1985). This approach is undoubtedly justified in natural and seminatural vegetation, where the importance of archaeophytes is minor. However, in man-made environments, the archeophytes represent a group of plants with specific ecology and pattern of behaviour in which they differ from both native species and later-immigrating neophytes. For that reason archaeophytes were treated as a separate group in this paper, and the term alien covers both them and neophytes, and is used strictly for any species not native to central Europe.

Data sources

Previously published floristic data were gathered for 54 European cities located within 48°13′–54°22′N and 6°45′–23°29′E (Table 1). The settlements with at least 5000 inhabitants were considered as towns/cities, also taking into account the town character.

Data on the number of species in particular categories of immigration status (i.e. native, archaeophyte, neophyte) were either given in the original source, or the species list was provided, in which case the classification was carried out for the purpose of the present study. For German cities the database of Frank & Klotz (1990) was followed, in the case of Czech and Polish cities it was defined by the use of local sources (Zajac, 1979; Opravil, 1980; Hejný & Slavík, 1988–92, Slavík, 1995). In the data which came from the biotope mapping of German cities ('STADTBIOTOPKARIERUNG – BRD' database, P. Werner, personal communication) those species with uncertain origin ('ohne Zuordnung') were not considered and not included into the calculation of percentages.

The immigration status in the original data sources is understood in geographical terms, i.e. the species native to the region were all considered as native. No account was therefore taken of the fact that in a particular city, native species may occur both in habitats which are close to being natural, as well as in habitats heavily transformed by man.

Each city was characterized by the number of inhabitants and city area, taken from respective papers or from demographical and statistical yearbooks and maps. Population density was calculated on the basis of these data. Where they were not given in the original source, the mean annual temperature, annual amount of precipitation and altitude were taken from climate diagrams (Walter & Lieth, 1967). If these were not directly available for a given city, the nearest one located in a similar geographical area was considered. Longitude and latitude were also recorded for each city.

The data were analysed using standard methods (Sokal & Rohlf, 1981). Because all environmental data were not available for each city, degrees of freedom may differ slightly in particular analyses. The difference in slopes on log–log axes was tested according to Snedecor & Cochran (1967).

RESULTS

Representation of alien and native species in Central European urban floras

On average, there were 87.4 archaeophytes, 172.4 neophytes (i.e. 259.7 alien species) and 386.5 native species in a city (Table 2). The number ranged between 30 and 167 in archaeophytes, 42–614 in neophytes, and 98–947 in native species (Table1). The total representation of aliens averaged 40.3% (minimum 19.7%, maximum 59.7%), with archaeophytes contributing 15.2% (6.5–28.0%) and neophytes 25.2% (10.9–47.5%).

Factors affecting the composition of urban floras

A regression of species numbers on particular environmental variables (Table 3) revealed highly significant increases in each of the categories of immigration status with city size, whether expressed as number of inhabitants or city area (Fig.1). For neophytes, the species–area relationship showed the highest slope *b* on log–log axes, the value of 0.49 being significantly higher ($F_{1,49}=11.21$, and $F_{1,49}=8.62$, respectively, $P<0.01$) than that for both archaeophytes (0.16) and native species (0.30). Considering total aliens gives a slope of 0.37, which does not differ significantly ($F_{1,49}=3.63$, $P>0.05$) from that recorded for native species.

Species numbers also increased with the density of human population and with mean annual temperature, and decreased with increasing altitude and longitude (Table 3). The proportion of archaeophytes was significantly decreased with city size and that of neophytes was positively correlated with this characteristic. Consequently, the percentage contribution of total aliens to the city flora did not show any relationship with city size. It was negatively correlated with latitude only (Table 3, Fig. 2).

The factors used to characterize the settlements included in the analyses were in some cases mutually correlated (see also Pyšek, 1993). There were highly significant correlations

TABLE 1. Overview of cities analysed in the present study. Arch: archaeophytes; Neoph; neophytes; Aliens: archaeophytes and neophytes considered together (see Methods section for definitions and sources of information for the parameters of city size).

		Number					Proportion			City size		
Town	Region	Arch	Neoph	Aliens	Native	Species total	Arch	Neoph	Aliens	Pop. (000s)	Area (km²)	Data source
Wien	Austria	134	614	748	728	1476	0.09	0.42	0.51	1600	414	Forstner & Hübl, 1971 (b)
Brno	Czech	148	281	429	335	764	0.19	0.37	0.56	344	200	Grüll, 1979 (a)
Horaždovice	Czech	49	51	100	305	405	0.12	0.13	0.25	6	23	Mandák, 1996 (b)
Kostelec	Czech	40	63	103	234	337	0.12	0.19	0.31	5	14	P. Pyšek, unpubl. data
Plzeň	Czech	77	154	231	299	530	0.15	0.29	0.44	171	95	Pyšek & Pyšek, 1988 (b)
Arnsberg	Germany	84	83	167	446	613	0.14	0.14	0.27	74	n.a.	Fischer *et al.* 1992*
Berlin (West)	Germany	167	410	577	841	1418	0.12	0.29	0.41	1930	480	Kowarik, 1988 (a)
Bochum	Germany	63	189	252	209	461	0.14	0.41	0.55	383	145	Schulte, 1985 (c)
Bremerhaven	Germany	42	52	94	384	478	0.09	0.11	0.20	137	80	Kunick, 1979 (b)
Darmstadt	Germany	128	245	373	593	966	0.13	0.25	0.39	134	128	Jung, 1992*
Dietzenbach	Germany	92	111	203	386	589	0.16	0.19	0.34	27	22	Gotzhein & Steinbach, 1985*
Essen	Germany	87	343	430	483	913	0.10	0.38	0.47	620	210	Reidl, 1989, Reidl & Dettmar, 1993 (c)
Euskirchen	Germany	70	108	178	359	537	0.13	0.20	0.33	45	10	Zimmermann-Pawlowsky, 1985 (b)
Frankfurt/M.	Germany	124	265	389	456	845	0.15	0.31	0.46	645	248	AG Biotopkartierung Frankfurt*
Hanau	Germany	113	208	321	455	776	0.15	0.27	0.41	85	77	Egel-Gessner & Werner, 1988*
Hannover	Germany	100	127	227	687	914	0.11	0.14	0.25	523	225	Haeupler, 1976 (b)
Karlsruhe	Germany	113	217	330	369	699	0.16	0.31	0.47	268	173	Kunick, 1985*
Köln	Germany	76	300	376	571	947	0.08	0.32	0.40	970	400	Kunick, 1983 (b)
Leipzig	Germany	135	439	574	745	1319	0.10	0.33	0.44	554	141	Gutte, 1989 (b)
Mannheim	Germany	102	181	283	287	570	0.18	0.32	0.50	296	145	Back *et al.* 1987*
Morfelden-Walldorf	Germany	114	165	279	442	721	0.16	0.23	0.39	30	44	Gessner, 1990*
Mühlheim a. Main	Germany	61	56	117	263	380	0.16	0.15	0.31	24	21	Rustler & Weiss, 1986*
Neu-Isenburg	Germany	85	124	209	377	586	0.15	0.21	0.36	35	24	Dombrowe, 1987*
Neumünster	Germany	54	75	129	352	481	0.11	0.16	0.27	83	72	Mordhorst *et al.* 1990*
Rüsselsheim	Germany	117	138	255	431	686	0.17	0.20	0.37	57	58	Asmus *et al.* 1981*
Saarlouis	Germany	103	105	208	366	574	0.18	0.18	0.36	38	43	Maas, 1985*
Stuttgart	Germany	128	372	500	947	1447	0.09	0.26	0.35	568	250	W. Kunick, pers. comm. (b)
Wiesbaden	Germany	105	158	263	486	749	0.14	0.21	0.35	267	204	Chevallerie *et al.* 1986*
Wuppertal	Germany	64	121	185	311	496	0.13	0.24	0.37	385	170	Kunick & Rohner, 1987, 1989*
Belchatow	Poland	93	100	193	313	506	0.18	0.20	0.38	54	35	Sowa & Warcholinska, 1980 (a)
Chelm	Poland	30	120	150	290	440	0.07	0.27	0.34	63	35	Fijalkowski, 1963 (a)
Gdansk	Poland	105	346	451	579	1030	0.10	0.34	0.44	373	242	Schwarz, 1967 ‡ (a)
Gorlice	Poland	65	67	132	149	281	0.23	0.24	0.47	29	24	Swies, 1984 † (a)
Jaroslaw	Poland	69	96	165	166	331	0.21	0.29	0.50	30	40	Swies & Piorecki, 1988 † (a)
Jaslo	Poland	57	97	154	122	276	0.21	0.35	0.56	37	37	Swies & Pleban, 1981 † (a)
Krosno	Poland	81	73	154	178	332	0.24	0.22	0.46	49	43	Swies, 1983 † (a)
Legnica	Poland	101	172	273	302	575	0.18	0.30	0.47	73	30	Aniol-Kwiatkowska, 1974 (c)
Lodz	Poland	78	178	256	291	547	0.14	0.33	0.47	753	214	Sowa, 1964 ‡ (a)
Lubin	Poland	95	88	183	291	474	0.20	0.19	0.39	28	14	Aniol-Kwiatkowska, 1974 (c)
Lublin	Poland	33	154	187	323	510	0.06	0.30	0.37	291	119	Fijalkowski, 1967 (a)
Opole	Poland	109	254	363	439	802	0.14	0.32	0.45	87	53	Michalak, 1970 ‡ (a)
Polkowice	Poland	74	45	119	168	287	0.26	0.16	0.41	8	8	Aniol-Kwiatkowska, 1974 (c)
Poznan	Poland	100	100	200	700	900	0.11	0.11	0.22	600	115	Jackowiak, 1990 (c)
Rabka	Poland	94	57	151	232	383	0.25	0.15	0.39	13	37	Skowronska, 1965 (b)
Rzeszow	Poland	68	77	145	98	243	0.28	0.32	0.60	151	60	Kucharczyk & Swies, 1988 (a)
Sandomierz	Poland	66	94	160	177	337	0.20	0.28	0.47	23	n.a.	Kucharczyk & Kucharczyk, 1984 † (a)
Sanok	Poland	58	69	127	325	452	0.13	0.15	0.28	20	22	Kucharczyk & Swies, 1988 (a)
Stalowa Wola	Poland	65	75	140	103	243	0.27	0.31	0.58	23	53	Kucharczyk & Swies, 1988 (a)
Szczecin	Poland	92	303	395	476	871	0.11	0.35	0.45	337	283	Cwiklinski, 1970 ‡ (a)
Szczercow	Poland	57	42	99	183	282	0.20	0.15	0.35	n.a.	n.a.	Sowa & Sicinski, 1982 (a)
Tarnobrzeg	Poland	63	71	134	164	298	0.21	0.24	0.45	30	20	Swies & Kucharczyk, 1982 † (a)
Tarnow	Poland	91	68	159	376	535	0.17	0.13	0.30	119	72	Kucharczyk & Swies, 1988 (a)
Warszawa	Poland	95	248	343	766	1109	0.09	0.22	0.31	1641	430	Sudnik-Wojcikowska, 1987 (a)
Wroclaw	Poland	103	559	662	515	1177	0.09	0.47	0.56	517	225	Krawiecowa & Rostanski, 1976 (a)

Sources: *data provided from the STADTBIOTOPKARIERUNG – BRD database (P. Werner, unpublished); †, cited by Kucharczyk & Swies (1988); ‡ cited by Krawieczova & Rostanski (1976). Nature of the data: (a) – species number in particular categories of immigration status was given in the original source; (b) calculated from the species list provided in the original sources; (c) species numbers estimated from figures or calculated from percentages. n.a., data not available

TABLE 2. Overview of representation of particular immigration status categories and comparison of German and Polish cities. Means ±SD are given. Temperature is characterized by annual average, precipitation by annual sum. The significance of difference in floristic composition between German and Polish cities is indicated. Df, *F*-value and significance level P are shown for main effects in ANOVA with significant predictors from multiple regression (see Table 3) used as covariates. The difference in city characteristics was tested by one-way ANOVA.

	Total data	Germany	Poland	Analysis of variance d.f.	F	P
Number of cities	54	24	25			
Floristic composition:						
Number of archaeophytes	87.4±29.4	97.0±29.7	77.7±21.7	1,40	0.17	0.898
Number of neophytes	172.4±130.0	191.3±111.9	142.1±119.5	1,43	0.73	0.407
Number of aliens	259.7±150.7	288.3±134.3	219.8±131.0	1,40	0.43	0.524
Number of native	386.5±195.2	468.6±181.4	309.0±181.8	1,41	0.33	0.578
Percentage of archaeophytes	15.2±5.3	13.5±2.9	17.3±6.5	1,45	5.10	0.028
Percentage of neophytes	25.2±8.6	24.2±7.9	25.6±8.7	1,41	1.94	0.171
Percentage of aliens	40.3±9.5	37.6±8.2	42.7±9.6	1,45	5.11	0.029
City characteristics:						
Population (thousands)		340.8±426.0	222.9±367.0	1,46	1.05	0.031
Area (km^2)		146.5±120.7	96.1±108.8	1,44	2.12	0.144
Altitude (m a.s.l.)		114.0±71.3	184.4±144.5	1,46	4.72	0.035
Temperature (°C)		9.4±0.6	7.9±0.4	1,46	109.69	<0.0001
Precipitation (mm)		700.4±140.6	619.3±101.5	1,46	5.32	0.025

TABLE 3. Regressions of particular categories of European urban flora on various environmental variables. Correlation coefficients (d.f. 1, 51) and their significance are shown for each variable.

	Population	Area	Density	Altitude	Latitude	Longitude	Temperature	Precipitation
Number of archaeophytes	0.48***L	0.51***L	0.29*L	−0.16 ns	−0.15 ns	−0.31*E	0.46***M	−0.08 ns
Number of neophytes	0.78***M	0.77***M	0.54***M	−0.36**E	−0.00 ns	−0.17 ns	0.42**M	−0.08 ns
Number of aliens	0.76***M	0.75***L	0.52***M	−0.32*E	−0.03 ns	−0.27*E	0.45***M	−0.08 ns
Number of native	0.70***L	0.71***L	0.54**M	−0.37**M	0.19 ns	−0.47***E	0.44**M	−0.07 ns
Proportion of archaeophytes	−0.54***M	−0.51***L	−0.42**L	0.39**M	−0.34*L	0.35*L	−0.24 ns	0.07 ns
Proportion of neophytes	0.45***M	0.47***M	0.31*M	−0.23 ns	−0.12 ns	0.07 ns	0.15 ns	−0.06 ns
Proportion of aliens	0.07 ns	0.13 ns	0.00 ns	−0.03 ns	−0.32*E	0.26 † L	0.01 ns	−0.03 ns

* P<0.05,** P<0.01,*** P<0.001, ns, nonsignificant, † marginally significant –0.05<P<0.07.
Models providing the best fit to the data are indicated: L, linear $Y = a + bX$, M, multiplicative $Y = aX^b$, E, exponential $Y = \exp(a + bX)$. See methods for definition of archaeophytes and neophytes.

in the data set between the parameters of city size (population–area 0.92, population–density 0.69, density–area –0.53) and between some geographical and climatic factors: temperature–altitude –0.35, temperature–longitude –0.86, latitude–altitude –0.53. There was also a significant relationship between city size and its altitude (r=–0.28 for the number of inhabitants, and r= –0.34 for city area) indicating that the bigger cities are located mainly in lowlands. To overcome this limitation in the data analysis, step-wise multiple regression was used to test for significant predictors (Table 4). The multiple regression explained between 40 and 65% of variation in the species numbers for particular categories of immigration status, providing the best fit for neophytes. City size was still the best predictor (P<0.001) for both species number and the proportion of archaeophytes and neophytes. The number of archaeophytes and that of total aliens was positively affected by temperature, another highly significant predictor (P<0.001). In addition, there were some relationships between the flora composition and geographical coordinates, though less significant (P<0.05): the number of neophytes and their proportion was decreasing with increasing latitude. In addition, the richness of native species in cities decreased with increasing longitude and that of aliens increased in dependence on this characteristic (Table 4).

Percentage of variability in the proportion of total aliens explained by the variables used was very low (8.2%), the only significant predictor was latitude. The higher this factor, the lower was the representation of aliens (Fig. 2).

Comparison of German and Polish cities: an effect of regions

To test the effect of region (country) in which the city was located, German cities (n=24) were compared with those in Poland (n=25). Concerning the natural conditions, the former are on average bigger, are located at lower altitudes, and have a higher annual temperature (Table 2). Although the German cities are generally richer in species, whatever

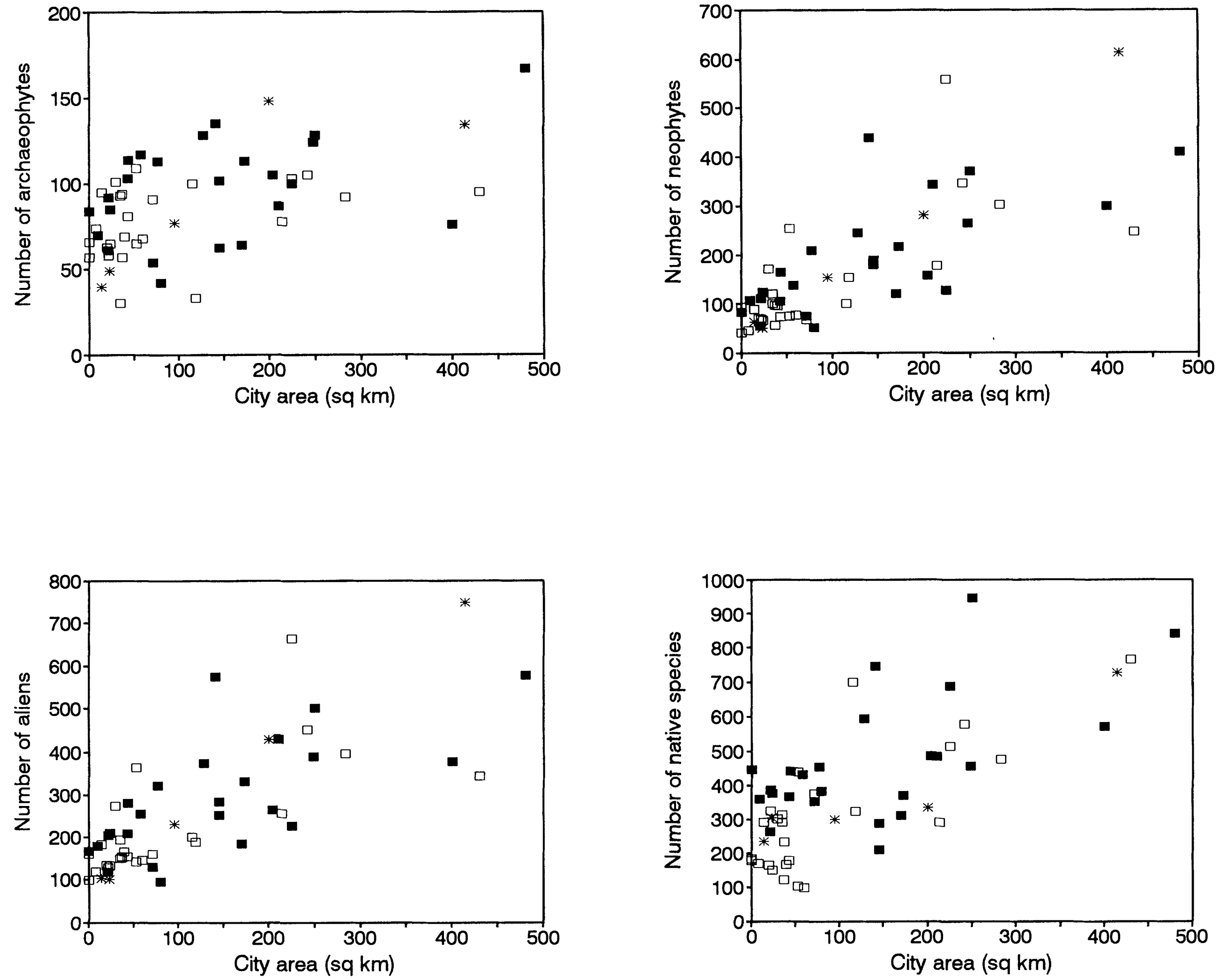

FIG. 1. Relationship between the number of species in particular categories of immigration status and city size, expressed by area. All regressions were significant at $P<0.001$, see Table 3 for statistical details. German cities are shown by solid squares, Polish by empty squares, and the others (Czech cities and Vienna) by asterisks.

category is taken into account (Table 2), the effect of region on species numbers was not significant.

Polish cities, however, had significantly higher ($P<0.05$) proportion of archaeophytes and of total aliens. The effect of region on the proportion of neophytes was not significant.

DISCUSSION

Urban areas generally exhibit a higher representation of aliens when compared to other habitat types (see, e.g. Crawley, 1987). In the Central European flora, as summarized in the list of Frank & Klotz (1990), there are, out of 2269 species, 6.8% archaeophytes, 19.7% neophytes and 73.5% native species. It seems reasonable to consider these figures as a reference data set for the floras analysed in the present paper. The comparison then reveals that the average percentage of aliens in Central European cities is 13.7% higher than their representation in the total species pool available in the region, indicating a remarkable concentration of aliens in urban areas. Compared to natural habitats, the difference is even more profound: the proportion of alien species (in the sense of the present paper) in selected Czech nature reserves, although exhibiting an increasing trend over time, varied between 1.7 and 15.2% (9.8% on average, Kučera, 1995).

In the present Central European landscape, the cities are therefore the habitat which are richest in alien species, and serve as an important source of aliens (often invasive) for smaller settlements and for further spread into the landscape. Pyšek (1998) found that the representation of aliens in Czech villages, i.e. settlements of rural character of up to 2000 inhabitants, was, beside the village size and altitude, negatively related to the distance from the nearest medium-sized (100 000–200 000 inhabitants) town.

Outside Europe, quantitative data on the performance of introduced species in urban habitats are rare. Rapoport (1991) reported on 12% of exotics from 508 species in Mexico City and wider surroundings. When only the urbanized part of the city was considered, the percentage of aliens reached 20%, still well below values recorded in European cities.

Particular categories distinguished with respect to immigration status exhibit rather a distinct pattern of

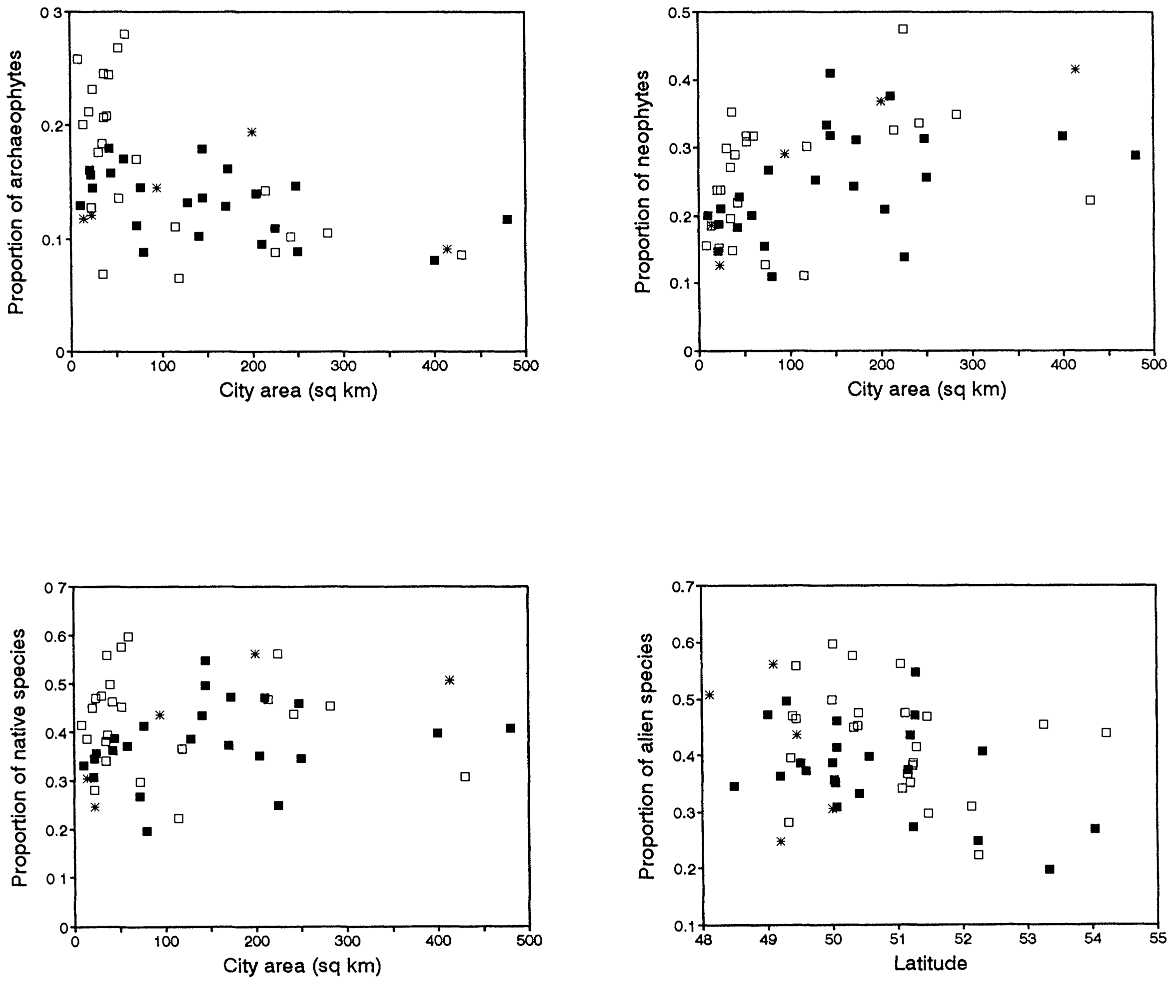

FIG. 2. Relationship between the proportion of particular categories of immigration status and city size, expressed by area. The regressions for archaeophytes and neophytes were significant at $P<0.001$, that of total aliens on area was non-significant (see Table 3 for statistical details). For total aliens, the only significant relationship ($P<0.05$), i.e. with latitude, is also shown. German cities are displayed by solid squares, Polish by empty squares, and the others (Czech cities and Vienna) by asterisks.

occurrence. The island effect (e.g. Begon *et al.*, 1986) was most pronounced with neophytes, whose log–log plotting gave the highest slope, indicating that aliens increase in number with city area more steeply than do both native species and archaeophytes. For neophytes, the surrounding landscape may be less favourable for survival because they are often dependent on humans as far as dispersal is concerned, or have higher temperature requirements that can be better met in big cities on behalf of the urban-heat-island effect (Sukopp & Werner, 1983; Gilbert, 1989). On the other hand, native species are probably more able to persist and spread in the landscape, even though it is disturbed and intensively managed. Similarly, Crawley (1987) found no species–area relationship for native species in floras of British counties but the plotting of aliens gave a slope which was significantly different from zero.

Not only the number of neophytes was increasing with city area, but their relative contribution to the total flora was also increasing. This reflects the fact that neophytes are the group which are most closely associated with human activity. On the other hand, archaeophytes are doing relatively better in smaller cities because they are being confined rather to a rural environment. Big cities which are usually highly industrialized provide fewer convenient habitats (old fields, arable land, etc.) for archaeophytes to persist, and at the same time the introduction and establishment of neophytes are encouraged, which phenomena both contribute to the lower representation of the former. For that reason, the proportion of aliens, composed of both these groups exhibiting opposite trends, does not show any relationship to city size (and nor does the proportion of native species).

Not surprisingly, archaeophytes and total aliens were especially strongly encouraged by higher temperatures, a result which reflects their origin in warmer regions, i.e. Mediterranean for the former and mostly Northern America and Asia for the latter (Wittig & Durwen, 1982; Sukopp & Werner, 1983; Lohmeyer & Sukopp, 1992). The performance of neophytes, and total aliens, expressed as a percentage contribution to the urban flora, was higher in the lower

TABLE 4. Summary of multiple regressions analysing the complex effect of environmental variables on the composition of central European urban flora. Non-significant predictors are not shown although used in the model. Log transformation of data is indicated when used

	Analysis of variance				Predictors									
					Population		Area		Latitude		Longitude		Temperature	
	R^2	d.f.	F-value	P-level	t	P	t	P	t	P	t	P	t	P
Number of archaeophytes	39.9	3,46	11.85	<0.0001		NS	3.69	0.0006		NS	2.36	0.0222 LOG	3.54	0.0009 LOG
Number of neophytes	63.9	2,47	44.41	<0.0001 LOG	9.41	<0.0001 LOG		NS	−2.28	0.0271		NS		NS
Number of aliens	64.9	3,46	31.22	<0.0001		NS	7.86	<0.0001		NS	3.13	0.0030 LOG	3.90	0.0003 LOG
Number of native	54.2	2,47	29.96	<0.0001		NS	6.91	<0.0001		NS	−2.19	0.0329		NS
Proportion of archaeophytes	27.1	1,48	19.21	0.0001	−4.38	0.0001 LOG				NS		NS		NS
Proportion of neophytes	25.2	2,47	9.25	0.0004 LOG		NS	4.14	0.0001	−2.04	0.0466		NS		NS
Proportion of aliens	8.2	1,48	5.35	0.0250 LOG		NS		NS	−2.31	0.0250		NS		NS

latitudes, presumably reflecting the flora depauperation in more northerly located areas. However, this relationship is rather vague and difficult to explain unequivocally; the same holds for the increase in aliens (and decrease of native species) with longitude.

The factors operating on big cities exhibit a somewhat different pattern from those determining the mutual proportion of aliens and native species in small villages (Pyšek, 1998). In the villages, both the proportion of archaeophytes and neophytes are increasing with village size. This difference indicates that, up to a particular intensity, human activities are encouraging archaeophytes in the same way as are neophytes; further increases in settlement size and associated increases in urbanization, however, result in the diminished importance of archaeophytes.

There was also an effect of region on the proportion of alien species, significant at the same level as was that of latitude. Polish cities exhibit higher proportion of archaeophytes and of total aliens and are both absolutely and relatively poorer in native species. Cultural differences, levels of industrialization, and historical background may serve as a possible explanation. German cities represent a highly industrialized environment, with a decades-long developed trade and communication with the rest of the world, therefore supporting rather neophytes whereas Polish cities are on average smaller, and of more rural character. A higher representation of native species in German cities could be the consequence of the approach to the urban environment. Germany is the leading European country in biotope mapping and urban ecology (Sukopp, 1990) and even the public are aware of the importance of nature in cities. In addition, different approaches applied by both research schools may play a role, being reflected, e.g. in the evaluating of immigrating status, delimitation of city boundaries, taking the fringe area into account, etc. (Pyšek, 1995c).

When analysing data sets such as those in the present paper, one must be aware of some data limitation. Particular data sets will undoubtedly differ in quality, depending on research duration and intensity (see Pyšek, 1993); in cities with a long tradition of botanical research, the data are probably more reliable. Unfortunately, these side-effects cannot be properly tested with the available data.

ACKNOWLEDGMENTS

My thanks are due to Peter Werner, Darmstadt, for providing me with the data from STADTBIOTOPKARTIERUNG-BRD database, and to Wolfram Kunick, Bornheim, for floristic data. Kind help from Jörg Dettmar, Ingo Kowarik, Konrad Reidl, Herbert Sukopp and Rüdiger Wittig is appreciated. I also thank two anonymous referees for their comments.

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