Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales

Zastoupení nepůvodních a původních dřevin v Berlíně závisí na typu stanoviště a prostorovém měřítku

Ingo K o w a r i k[1, 2], Moritz v o n d e r L i p p e[1, 2] & Arne C i e r j a c k s[1, 2]

[1]*Department of Ecology, Technische Universität Berlin, Rothenburgstr. 12, D 12165 Berlin, Germany, e-mail: kowarik@tu-berlin.de, moritz.vdlippe@tu-berlin.de, arne.cierjacks@tu-berlin.de;* [2]*Berlin-Brandenburg Institute of Advanced Biodiversity Research (BBIB), 14195 Berlin, Germany*

Kowarik I., von der Lippe M. & Cierjacks A. (2013): Prevalence of alien versus native species of woody plants in Berlin differs between habitats and at different scales. Preslia 85: 113–132.

Cities are hotspots for plant invasions and woody plants that have escaped from cultivation contribute significantly to this phenomenon. Yet whether the richness of alien species in the floras of woody plants in urban areas also corresponds to a prevalence of alien species at the habitat and population levels is an open question. To explore the scale and context dependence of invasions by woody plants of urban environments, we analysed the occurrence of alien and native species of trees, shrubs and vines at the city, habitat and community scales in Berlin, Germany. The percentage of alien species in the flora of spontaneously occurring woody plants increased from 16% at the end of the 18th century to 67% two hundred years later. Of the 181 species of alien woody plants in Berlin's flora 32% have become naturalized. Species from other parts of Europe, the Mediterranean and western Asia escaped and became naturalized more frequently than species from other areas. Escape from cultivation did not increase the share of evergreens in the total flora of woody plants. All habitats other than wetlands had more alien than native species, and the percentage of alien species was significantly higher in green spaces, wastelands and residential areas than in forests and wetlands. However, native species were more frequent at the habitat scale. Overall, the trees most likely to be found in all habitats were native *Acer platanoides*, *Betula pendula*, *Quercus robur* and alien *Robinia pseudoacacia*, *Acer negundo* and *Prunus serotina*, and the most frequent shrubs the native *Sambucus nigra* and alien *Mahonia aquifolium*. At the community scale, counts of the numbers of individual trees in two selected study areas revealed that native species prevailed in residential areas and alien species in urban wasteland. The results demonstrate that invasion success of alien woody species in urban environments is strongly scale- and context-dependent. The clear dominance of alien species in the total urban species pool was not similar at both the habitat and community scales, particularly when the frequency of species is considered. In conclusion, assemblages of woody species in urban areas are not only characterized by high numbers of aliens but also by an increase in the abundance of native species such as the formerly rare *Acer platanoides* and *A. pseudoplatanus*, which now prevail due to enhanced propagule pressure and the eutrophication of urban ecosystems.

K e y w o r d s: *Ailanthus altissima*, casual species, exotic species, functional traits, naturalization, non-indigenous plant, ornamental species, urban heat island

Introduction

All over the world, urban regions are hotspots in terms of the wealth of woody species that are cultivated there. Studies on parks (Zhao et al. 2010, Nagendra & Gopal 2011, Abendroth et al. 2012), domestic gardens (Ringenberg 1994, Akinnifesi et al. 2010) and tree plantings along streets (Jim & Chen 2008, Nagendra & Gopal 2010, Sjöman et al.

2012) reveal that among the cultivated plants there is a high percentage of alien species of trees. In the plantings in green spaces in Hong Kong, China and Christchurch, New Zealand, for example, 73–84% of the trees are alien species (Jim 2000, Stewart et al. 2004). Alien species also dominate the woody species cultivated in European landscape parks (66% is the mean for three parks; Säumel et al. 2010). In Patras, Greece, introduced species make up 59–75% of the planted woody species pool in various urban landscapes (Tsiotsiou & Christodoulakis 2010).

Planting large numbers of non-native ornamentals usually results in a strong propagule pressure in urban regions, which is an important driver of the subsequent naturalization of these species (Mulvaney 2001, Kowarik 2005, Lockwood et al. 2005, Křivánek et al. 2006, Pyšek et al. 2009). Correspondingly, the frequency of species offered for sale by the horticultural trade is associated with their later success in escaping from cultivation (Dehnen-Schmutz et al. 2007). As a consequence, cities are usually rich in alien species (Kowarik 1995a, Pyšek 1998) of which escaped woody species are an important part. Moreover, the steady supply from garden centres of semi-hardy plants from warmer regions along with global warming is believed to foster the escape of these species from cultivation in many parts of Europe (Niinemets & Peñuelas 2008).

The escape of ornamentals from cultivation can be enhanced by urban conditions, in particular by urban heat island effects, which amplify the effects of global warming. As a consequence, phenological changes such as earlier bud burst or flowering are recorded in cities (Zacharias 1972, Roetzer et al. 2000, Shustack et al. 2009, Neil et al. 2010). The interplay between urban heat islands, global warming and increased cultivation of alien species may foster the establishment of plant species from functional groups that were previously under-represented in a region. A comparable example from natural habitats is the increased spread of evergreen ornamentals in some regions associated with the temperature increase recorded during the last decades (Walther 2002, Walther et al. 2009). Also species with other traits, such as animal dispersal, are over-represented in urban compared to rural floras (Knapp et al. 2008, 2010). In New York, more alien than native species of woody plants have fleshy fruits (Aronson et al. 2007), likely due to gardeners' preferences for species with shiny fruits (Knapp et al. 2009). There are other factors that enhance the naturalization of introduced species in urban settings. Maintenance activities such as irrigation can help protect juvenile plants from detrimental environmental effects (Mack 2000), and tree plantings can facilitate population establishment by overcoming spatial separation from adequate but otherwise inaccessible sites (Kowarik 2003).

Historical analyses of urban floras published over periods of decades and centuries reveal a marked increase in the number of woody species (Chocholoušková & Pyšek 2003, Knapp et al. 2010, Zhao et al. 2010, Gregor et al. 2012). This historical increase in alien species richness goes along with an increase in the ranges of alien woody species in urban landscapes over time as is recorded for the New York metropolitan region (Aronson et al. 2007).

At the habitat scale, most studies on woody species focus on forest remnants, either addressing the establishment of native species (e.g. Lehvävirta & Rita 2002, Hauru et al. 2012), their role as sources of propagules for the reestablishment of native species in urban areas (e.g. Doody et al. 2010) or invasion by alien species from urban areas (Bertin et al. 2005, Borgmann & Rodewald 2005, Duguay et al. 2007, Essl et al. 2011). There are few studies on urban green spaces (Stewart et al. 2004), residential areas (Ringenberg 1994, Stewart et al. 2004), wastelands (Kowarik 1990a, Trentanovi et al. 2013) or walls and buildings (Jim 2008, Jim & Chen 2011). Comparative studies of the woody species that have escaped cultivation occurring in several habitats, however, are rare (but see Kunick 1987, Stewart et al. 2009, Tsiotsiou & Christodoulakis 2010, Nowak 2012).

Escape from cultivation is an important conservation issue because urban plantings can function as invasion foci for the spread of alien species into adjacent landscapes (Sullivan et al. 2005, Vidra & Shear 2008), although studies of this risk have yielded ambiguous results (Botham et al. 2009, Kowarik 2011). Moreover, plantings of native species could provide a source of propagules for the (re)establishment of native woody vegetation in urban habitats (Stewart et al. 2004, Doody et al. 2010, Woodall et al. 2010). Finally, novel assemblages of urban species, which may be well adapted to urban conditions and provide cities with a range of ecosystem services (Kowarik 2011), may be shaped by escapees. Yet, as Lehvävirta (2007) states, there are significant gaps in our knowledge of the regeneration of assemblages of urban woody species and the underlying mechanisms.

Taking the city of Berlin, Germany, as an example of a central-European metropolitan region, we explored native and alien species in pools of woody plants at different scales. (i) At the city scale, we analysed the richness of native and alien species of woody plants and changes in the percentage of alien species since the 18th century, and (ii) tested whether the origins of the woody plants that have escaped cultivation in Berlin reflect the origins of all the introductions of woody species into central Europe. (iii) As alien species are known to change the composition of urban floras in terms of functional traits (Aronson et al. 2007, Knapp et al. 2009), we analysed changes since the 18th century in the representation of life forms and evergreen species within the flora of woody plants. (iv) To determine whether the occurrence of species in different urban habitats is uneven (Lososová et al. 2011), we assessed the number and frequency of woody species in five major urban habitats for which we calculated the percentage of alien species (v). To determine whether these percentages are the same at the city, habitat and community scales, we analysed two datasets from selected study areas in which there were trees in different vegetation layers.

Methods

Study area and data sources

The study area was Berlin, Germany, which has a population of about 3.5 million and covers an area of 892 km^2. The prevailing natural vegetation is deciduous forest. Near-natural forest remnants growing mostly on sandy acidic soils at the urban fringe are dominated by *Quercus robur, Q. petraea*, *Pinus sylvestris* and by *Alnus glutinosa* on wet sites (Sukopp 1990). Currently, about half of Berlin's surface consists of built-up areas, 20% is forested, green spaces make up 10%, moving and standing water 6% and agricultural land 7% (SenStadt 2008).

The long history of floristic research in Berlin offers excellent opportunities for assessing changes in the flora of woody plants (Sukopp 1987, Krausch & Sukopp 2010). Regional horticultural and silvicultural literature provides records of cultivation starting in 1594 (e.g. Franke 1594, Elssholtz 1663). The flora of Willdenow (1787) first differentiated between cultivated and spontaneously occurring species and subsequent floras provide plenty of information on the latter (e.g. Ascherson 1864, Bolle 1887). Since the

1970s, there have been ecological studies on almost all near-natural and urban land use types in Berlin, which include a substantial amount of data on native and alien species at the habitat scale (see syntheses by Sukopp 1990, Kowarik 1992).

The origins of escaped species were determined by using data from Goeze (1916), Fitschen (1987) and Meusel et al. (1965, 1978). The compilation by Goeze (1916) also provides data on the regions of origin of 2645 species of woody plants introduced into central Europe up to the beginning of the 20th century. This allowed us to test whether the origins of the species of woody plants that have escaped and possibly naturalized in Berlin match that of all central-European introductions of species of woody plants.

To explore changes in the composition of life forms in the flora of woody plants, we relied on the classification of Fitschen (1987) of tall, medium-sized and small trees, tall and small shrubs, dwarf shrubs, half-shrubs and woody vines, and the same source was also used to distinguish species with evergreen or deciduous leaves. Both traits are relevant as leaf persistence and the capacity of a species to grow tall are often associated with invasion success (Reichard & Hamilton 1997, Pyšek & Richardson 2007). We calculated their representation in native and all escaped alien species, and separately for naturalized species, i.e. the subcategory of alien species with records of at least two spontaneous generations over a period of at least 25 years (Kowarik 1992). Alien species consist of archaeophytes (pre-1492 introductions) and neophytes (post-1492 introductions; Richardson et al. 2000). The nomenclature follows Fitschen (1987).

To assess numbers of species and frequency of native and alien species of woody plants at the habitat scale, we used existing data on species occurrence in five groups of habitat types (hereafter 'habitats'): (i) remnants of natural forest (without wetlands; 405 phytosociological relevés from a larger data set; Kowarik 1990b), (ii) near-natural wetlands (peat, swamp woods; 201 relevés from a larger data set; Kowarik 1990b), (iii) urban green spaces (parks, cemeteries etc.; 221 relevés from eight studies), (iv) urban wastelands (abandoned railway areas, brownfields etc.; 151 relevés from 11 studies), (v) urban residential areas (courtyards, domestic gardens, paved habitats in densely built-up areas, etc.; 405 relevés from six studies). The data, which consisted mostly of results from unpublished research reports and theses (see Kowarik 1992 for references), were used to assess species richness of native and alien trees, shrubs and woody vines in each habitat. Then, frequency data from these studies were combined for each species for each habitat. To allow for comparisons of the relative frequency of species among habitats, the value for the most frequent native or alien species was set at 100% for each habitat and the frequencies of all other species standardized to this maximum value.

Finally we illustrated the performance of native and alien species of tree at the community scale by analysing two data sets from different areas, which include numbers of individuals (or ramets in species with clonal growth; for reasons of simplicity we henceforth refer to both as 'individuals'). The first data set is for a densely built-up part of the historical centre of Berlin (Spandauer Vorstadt, Berlin-Mitte; 46.2 ha; data from Mücke & Kliese 1991); the second is for woodland on urban wasteland, which is dominated by self-sown alien *Robinia pseudoacacia* trees (28 plots 10 × 10 m; data from Kowarik 1990a). In both surveys, the total number of spontaneously growing individuals of native and alien species of trees was counted in the herbaceous (< 0.9 m), shrub (0.9–5.0 m) and tree layers (> 5 m).

Statistical analyses

Numbers of species and individuals were summarized in two-way contingency tables, which cross-classify the status as native/alien or as naturalized/non-naturalized (based on the difference in the numbers of escaped and naturalized species) versus the region of origin (Table 1), life form (Table 2), leaf persistence, habitat (Table 3) and vegetation layer (Table 6). In addition, we prepared contingency tables with the status introduced/escaped and introduced/naturalized cross-classified to the species' origin. These tables were used to fit log-linear models with and without a possible interaction between the two categories. Significant differences between the reduced model (model without interaction) and the full model (with interaction) along with a lower Akaike Information Criterion (AIC) in the full model indicated a significant interaction (Quinn & Keough 2003). In case of significant interactions, we used Cohen-Friendly association plots to detect a deviation from independence of a factor combination (Adler 2010). All statistics were calculated in R version 2.15.0 (The R Foundation for Statistical Computing 2012).

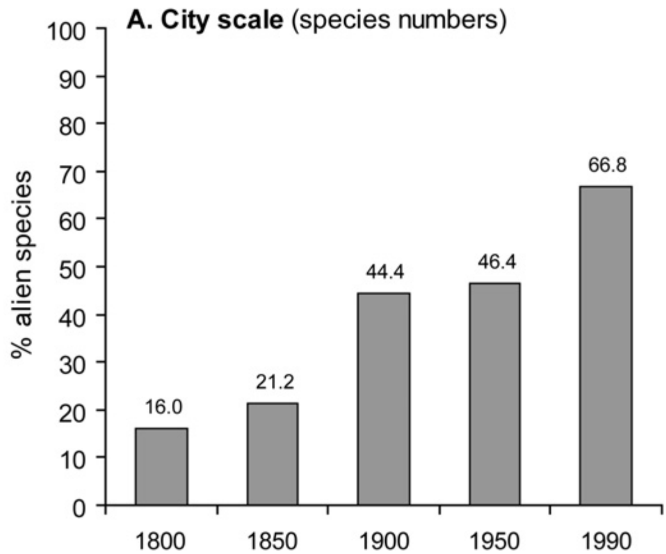
Results

City scale

Seventeen species of escaped woody plants that are alien to Berlin were recorded in the flora of Willdenow in 1787. Among these are fruit trees (e.g. *Prunus cerasus*, *Malus domestica*) that have been cultivated since medieval times and some ornamentals first cultivated more than 100 years before in the Berlin's palace garden (e.g. *Aesculus hippocastanum*, *Syringa vulgaris*; Elssholtz 1684). By the 1990s, the number of alien species had increased nearly 11-fold to 181 species of woody plants that had escaped cultivation. This number is twice that of species of woody plants native to Berlin (89 species). The percentage of alien species increased from 16.0% at the end of the 18th century to 66.8% at the end of the 20th century (Fig. 1A). Almost one-third (31.5%) of all escapees have naturalized in Berlin (57 species).

Other regions of Europe and the Mediterranean are the most important donor areas for escaped woody plants in Berlin (37.3%), followed by North America and other parts of Asia (Table 1). The log-linear model showed a significant interaction between the origins of alien species and their status as introduced/escaped ($G^2 = 161.64$, df = 5, $P < 0.001$, AIC reduced model = 294.9, AIC full model = 173.0). Likewise, we found a significant interaction between the origin of aliens and their status as introduced/naturalized ($G^2 = 85.61$, df = 5, $P < 0.001$, AIC reduced model = 212.4, AIC full model = 166.3). In both models, the number of escapees and naturalized species, respectively, was significantly higher than expected for species from Europe and western Asia and lower for species from other donor areas (Table 1).

In nearly all of the categories of life forms in the total woody flora of Berlin there were higher numbers of alien than native species (except dwarf and half shrubs, Table 2). Among alien species, shrubs were the prevailing life form (57%), but among naturalized species, trees and shrubs contributed equally. The log-linear models showed no significant interaction between life form and the alien/native or naturalized/non-naturalized status. We thus found no evidence for shifts in life forms within the urban flora of woody plants



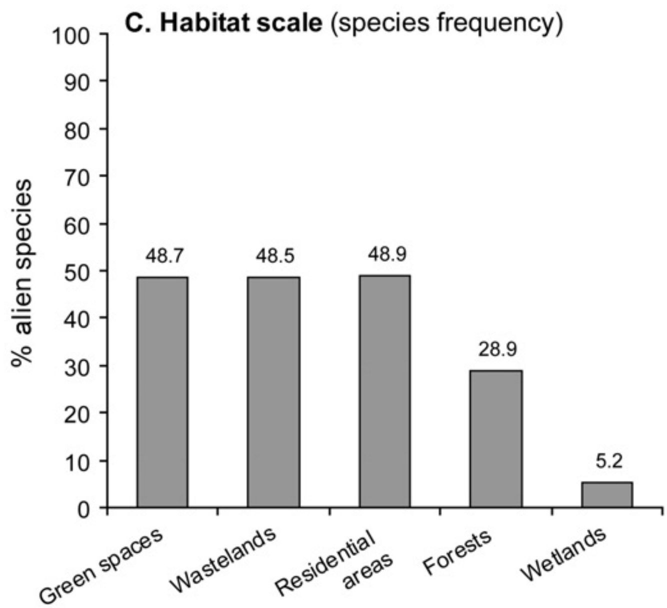
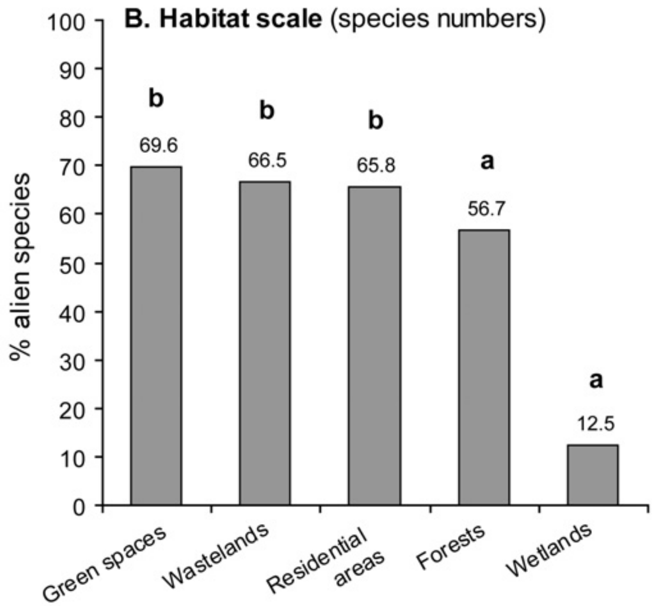


Fig. 1. – Percentages of alien species of woody plants in Berlin at different temporal and spatial scales; (A) city scale: changes in the percentage since the 18th century; (B) habitat scale based on numbers of species: percentages calculated for five habitats; (C) habitat scale based on species frequency; (D) community scale: percentages calculated for *Robinia pseudoacacia* woods in urban wastelands and an inner-city district (Spandauer Vorstadt), based on the number of individuals or ramets in different demographic stages (i.e. herbaceous, shrub, tree layers). Lower case letters refer to groups that deviate similarly in terms of their status as either alien or native species and habitat or vegetation layer from independence based on the Cohen-Friendly association plots. See text for further details.



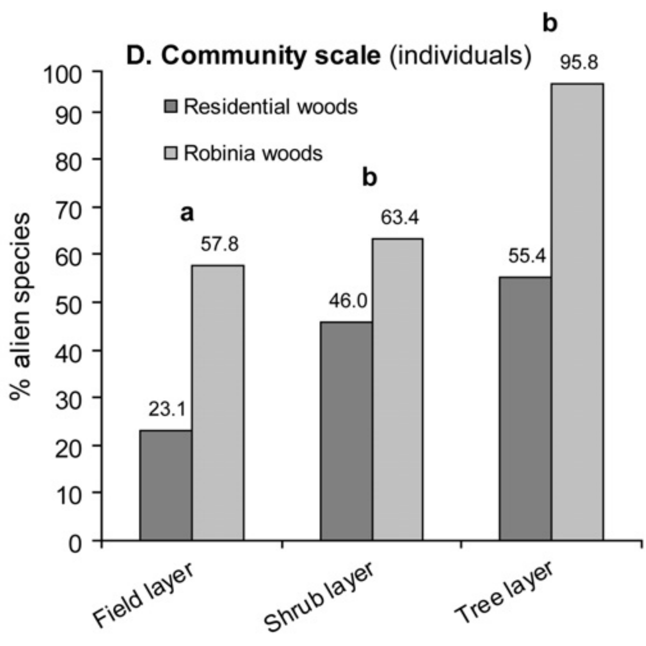


Fig. 1. – Continued

due to escape from cultivation or naturalization. The same holds for evergreen species, which made up almost the same percentage of native species (15.9%) as of escaped (15.7%) and naturalized (14.8%) alien species.

Table 1. – Origins of the species of woody plants introduced into central Europe (calculated using data from Goeze 1916) and invasion success of these species in Berlin, Germany (escaped, naturalized species; multiple entries for species that originate from more than one area; including *Rubus* species). Species numbers (n) and percentages of the total (%) are given.

Origin	Introduced into central Europe		Escaped in Berlin		Naturalized in Berlin	
	n	%	n	%	n	%
Europe, nemoral zone	122	4.6	51	21.6	19	23.5
Europe, meridional zone	187	7.1	37	15.7	16	19.8
Western Asia (incl. Caucasus, Taurus)	128	4.8	32	13.6	14	17.3
Central and northern Asia	304	11.5	11	4.7	5	6.2
Eastern Asia (incl. Himalayas)	1047	39.6	37	15.7	9	11.1
North America	857	32.4	58	24.6	16	19.8
Unknown or horticultural origin	n.a.		10	4.2	2	2.5
Total	2645		181		57	

Table 2. – The different life forms recorded in the flora of woody plants of Berlin. Data are shown for native species and escaped alien species, naturalized species are a subgroup of the latter (without *Rubus*). Species numbers (n) and percentages of the total (%) are given. Because a species may exhibit more than one life form additions of the values for the subcategories do not add up to the totals for each category.

Life form	Native		Escaped		Naturalized	
	n	%	n	%	n	%
Total tree species	29	42.0	68	39.5	26	48.1
Tall trees	19		32		10	
Medium sized trees	9		23		9	
Small trees	14		40		13	
Total shrub species	38	55.1	98	57.0	26	48.1
Large shrubs	25		59		21	
Small shrubs	15		51		11	
Dwarf shrubs	6		5		0	
Half-shrubs	4		3		1	
Woody vines	2	2.9	6	3.5	2	3.7
Total woody species	69	100	172	100	54	100

Habitat scale

The flora of the more urbanized habitats (green space, wasteland, residential) was much richer in spontaneously occurring species of woody plants than that of near-natural habitats (Table 3). More than 170 species were recorded in both wastelands and green spaces; even in residential areas more species (155) occurred than in near-natural forests (141) or wetlands (40).

Table 3. – Richness of species of woody plants in urban habitats in Berlin (n) and percentage of native (%N) and alien species of woody plants (%A). Data are shown for all species of woody plants (including vines) and for trees and shrubs. Values calculated from presence/absence data (100% is the total number of species for a habitat) and from frequency data (100% is the sum of all the frequencies of all native, or alien, species in each habitat) are shown.

		All species			Trees			Shrubs		
Habitat type	Measure	n	%N	%A	n	%N	%A	n	%N	%A
Green spaces	presence/absence	171	30.4	69.6	85	31.8	68.2	81	28.4	71.6
	frequency		51.3	48.7		56.9	43.1		42.8	57.2
Wastelands	presence/absence	173	33.5	66.5	76	38.2	61.8	92	29.3	70.7
	frequency		51.5	48.5		56.0	44.0		49.9	50.1
Residential areas	presence/absence	155	34.2	65.8	69	40.6	59.2	81	28.4	71.6
	frequency		51.1	48.9		60.0	40.0		39.0	61.0
Forests	presence/absence	141	43.3	56.7	67	43.3	56.7	70	42.9	57.1
	frequency		71.1	28.9		70.7	29.3		74.4	25.6
Wetlands	presence/absence	40	87.5	12.5	22	81.8	18.2	18	94.4	5.6
	frequency		94.8	5.2		93.5	6.5		96.3	3.4

Across all habitats and life forms, except for wetlands, the number of alien species exceeded that of native species of woody plants. About two-thirds of the species recorded in green spaces, wastelands and residential areas were alien, with a higher percentage of introduced species of shrubs compared to trees. Consistently, the log-linear model showed a significant interaction between habitat and the status as native or alien ($G^2 = 50.77$, df = 4, $P < 0.001$, AIC reduced model = 148.1, AIC full model = 123.4) with a higher percentage of alien species than expected in the three more urbanized habitats compared to the two near-natural habitats.

Considering the frequencies of species in the different habitats, alien species were less prominent in urban environments (Table 3, Fig. 1C). Native species clearly prevailed in wetlands and forests and were also more frequent than aliens in the more urbanized habitats. While native species of trees were generally more frequent in all the habitats, alien species of shrubs dominated in green spaces and residential areas.

Table 4 ranks native and alien species of trees according to their relative frequency in the five habitats. In the top rank are native tree species (*Acer platanoides*, *Betula pendula*, *Quercus robur*, *A. pseudoplatanus*), which were the species most likely to be found in all the habitats except wasteland, where the North American *Robinia pseudoacacia* was most frequent. Other highly frequent alien species of trees were *Acer negundo* (all habitats except wetland), *Prunus serotina* (mostly in forests and degraded wetlands), *Aesculus hippocastanum* (mostly in residential areas), *Quercus rubra* (mostly in green spaces) and *Ailanthus altissima* (mostly in residential areas and wasteland).

Similarly to trees, native species of shrubs were more frequent in all habitats than alien species of shrubs, with *Sambucus nigra* and three *Rubus* species at the top of the list (Table 5). *Mahonia aquifolium,* a cultivated hybrid complex of different North American species (Ross & Auge 2008), was the most common alien species of shrub (mostly in residential areas and green spaces), followed by *Syringa vulgaris* and *Symphoricarpos albus*. *Ribes uva-crispa* was the most frequent alien species of shrub in forests. In wetlands, alien species of shrubs only played a minor role, with *Cornus stolonifera* rarely established adjacent to the reed zones in riparian systems.

Table 4. – Relative frequency of spontaneously occurring native and alien species of trees in the five habitats in Berlin. Species that are alien to Berlin are in bold. The values are frequency numbers for the different studies, which were combined for each of the five habitats. In order to compare the relative frequencies in the different habitats the maximum frequency of a species in a habitat was set at 100. Shown are species with a relative frequency ≥ 10 in at least one habitat (Kowarik 1992). Species are ranked according to their mean frequency value (sum of habitat frequencies divided by 5) in all habitats. * Mostly did not include the planted individuals in the tree layer.

	Green spaces	Wastelands	Residential areas	Forests	Wetlands	Mean frequency
Acer platanoides	100	88	100	100	2	78
Betula pendula	81	91	78	29	100	76
Quercus robur	69	65	47	67	68	63
Acer pseudoplatanus	81	86	90	56	2	63
Robinia pseudoacacia	67	100	56	37	1	52
Acer negundo	70	70	56	38	3	47
Sorbus aucuparia	55	40	45	86	8	47
Prunus serotina	37	50	22	92	27	46
Pinus sylvestris	17	21	12	34*	91	35
Aesculus hippocastanum	34	32	63	37	0	33
Crataegus monogyna	26	74	39	24	1	33
Salix caprea	15	49	69	9	12	31
Quercus rubra	57	31	19	37	1	29
Ulmus glabra	39	53	38	14	0	29
Acer campestre	51	48	25	18	0	28
Tilia cordata	27	35	40	37	0	28
Ailanthus altissima	38	44	52	2	0	27
Populus tremula	4	56	32	26	12	26
Fraxinus excelsior	36	35	15	25	7	24
Carpinus betulus	29	26	21	35	0	22
Prunus padus	28	33	22	19	7	22
Populus alba* et *canescens	10	61	20	5	0	19
Prunus avium	20	28	31	15	0	19
Quercus petraea	17	13	<1	50	9	18
Malus domestica	13	34	32	9	0	18
Taxus baccata	38	11	22	5	0	15
Alnus glutinosa	6	8	2	9	49	15
Populus ×canadensis	7	44	13	6	0	14
Fagus sylvatica	9	1	6	54	0	14
Betula pubescens	0	13	0	7	49	14
Salix ×rubens	6	21	6	4	24	12
Prunus domestica	13	19	20	5	0	11
Pyrus communis	10	23	17	5	0	11
Juglans regia	19	16	15	5	0	11
Tilia platyphyllos	21	17	6	11	0	11
Prunus mahaleb	8	36	7	3	0	11
Laburnum anagyroides	18	14	20	2	0	11
Salix alba	2	29	11	3	7	10
Ulmus laevis	7	11	9	13	3	9
Ulmus minor agg.	8	21	8	4	0	8
Prunus cerasus	10	8	17	<1	0	7
Sorbus intermedia	6	22	0	1	0	6
Celtis occidentalis	2	19	3	0	0	5
***Populus nigra* 'Italica'**	7	10	4	0	0	4
Ulmus pumila	13	3	4	0	0	4
Hippophae rhamnoides	1	16	1	1	0	4
Elaeagnus angustifolia	2	12	1	1	0	3
Larix decidua	3	0	0	10	0	3
Quercus cerris	1	10	0	0	0	2

Table 5. – Relative frequency of spontaneously occurring native and alien species of shrubs in five habitats in Berlin. Species that are alien to Berlin are in bold. The values are frequency numbers in each of the studies, which were combined for each of the five habitats. In order to compare the relative frequencies of the species in each of the habitats the maximum frequency of a species in a habitat was set at 100. Shown are those species with a relative frequency ≥ 10 in at least one habitat (Kowarik 1992). Species are ranked according to their mean frequency value (sum of habitat frequencies divided by 5) for all habitats.

	Green spaces	Wastelands	Residential areas	Forests	Wetlands	Mean frequency
Sambucus nigra	100	100	100	100	11	82
Rubus idaeus	20	49	15	97	27	42
Rubus fruticosus agg.	38	69	14	64	4	38
Rubus caesius	23	90	6	51	4	35
Mahonia aquifolium	75	37	49	9	0	34
Rosa canina	28	83	24	34	0	34
Cornus sanguinea	28	57	21	26	0	26
Syringa vulgaris	27	52	40	11	0	26
Symphoricarpos albus	29	46	25	26	0	25
Euonymus europaea	31	48	9	33	0	24
Corylus avellana	33	23	38	24	0	24
Ligustrum vulgare	30	50	17	20	0	23
Frangula alnus	4	6	1	46	53	22
Vaccinium oxycoccos	0	0	0	<1	100	20
Philadelphus coronarius	16	34	33	7	0	18
Ribes rubrum	19	26	10	20	0	15
Lycium barbarum	21	38	10	5	0	15
Cornus stolonifera	13	24	16	7	12	14
Prunus persica	3	20	40	3	0	13
Ribes alpinum	17	20	16	11	0	13
Salix aurita	2	0	0	3	56	12
Lonicera tatarica	13	34	8	4	0	12
Ribes aureum	8	41	5	3	0	11
Lonicera xylosteum	21	17	5	11	0	11
Ribes uva-crispa	33	30	15	35	0	11
Colutea arborescens	2	35	4	1	0	8
Vinca minor	27	5	0	5	0	8
Salix cinerea	1	13	2	4	17	7
Cornus alba	13	20	1	2	0	7
Rosa rugosa	5	21	6	3	0	7
Viburnum lantana	10	11	9	3	0	7
Viburnum opulus	5	4	16	9	1	7
Buddleja davidii	4	6	23	0	0	7
Cytisus scoparius	1	19	3	5	0	6
Sambucus racemosa	2	2	1	23	0	6
Vaccinium myrtillus	2	0	0	25	0	5
Berberis vulgaris	8	10	2	5	0	5
Prunus spinosa	0	12	3	8	0	5
Salix purpurea	1	13	1	2	6	5
Rosa corymbifera	0	21	<1	1	0	4
Salix triandra	0	0	0	3	19	4
Sorbaria sorbifolia	3	1	15	1	0	4
Rubus laciniatus	5	14	0	<1	0	4
Rosa rubiginosa	2	12	4	<1	0	4
Calluna vulgaris	3	0	0	10	4	3
Caragana arborescens	12	8	14	2	0	3

Community scale

The sampling of species of trees in *Robinia* woods undergoing succession in a residential area revealed similar numbers of native and alien species of trees when the total species richness and numbers in each of the three vegetation layers were compared. In terms of abundance, native species of trees strongly prevailed in the residential area and alien species were more abundant in the *Robinia* woods (Table 6).

In both samples, about 90% of all the individuals occurred as seedlings or young saplings in the herbaceous layer. In the residential area, native species of trees clearly prevailed in the herbaceous layer, but this dominance was not pronounced in the shrub and tree layers. In contrast, alien species of trees dominated in all layers in the *Robinia* woods (Table 6). For both surveys, log-linear models showed a significant interaction between vegetation layer and whether the individual trees were alien/native ($G^2 = 35.34$, df = 4, $P < 0.001$, AIC reduced model = 100.8, AIC full model = 79.9 for residential area; $G^2 = 213.81$, df = 2, $P < 0.001$, AIC reduced model = 294.1, AIC full model = 97.9 for urban wastelands). The shrub and tree layers consistently had a higher number of individuals of alien species, whereas in the herbaceous layer the number was lower than expected.

Table 6. – Number of species and population sizes of alien and native species of trees in (A) a residential area in the historical centre of Berlin (Spandauer Vorstadt, 46.2 ha; adapted from Mücke & Kliese 1991) and (B) woods in urban wastelands dominated by *Robinia pseudoacacia* (0.28 ha; adapted from Kowarik 1990a). Shown are numbers of individuals (or ramets for species with clonal growth) per hectare in the herbaceous (> 0.9 m), shrub (0.9–5.0 m) and tree layers (> 5.0 m). In addition, data for the three most abundant native and alien species of trees in each study area are shown, with total counts in bold. The share of alien species refers to the abundance of alien and native species of trees.

	A. Residential area				B. *Robinia* woods			
Layer	Herb	Shrub	Tree	Total	Herb	Shrub	Tree	Total
Alien trees								
Species number	17	19	9	20	10	7	5	11
Individuals (n)	291	51	13	355	12,668	657	971	14,296
Individuals (%)	81.9	14.5	3.6	100.0	88.6	4.6	6.8	100.0
Most abundant:								
Ailanthus altissima	146	30	7	**184**	0	0	0	0
Acer negundo	67	11	3	**81**	6050	114	32	**6196**
Aesculus hippocastanum	37	0.4	0.3	**38**	0	0	0	0
Robinia pseudoacacia	14	4	1.4	20	3000	464	918	**4382**
Prunus serotina	0.1	0.4	0	0.5	1886	29	0	**1914**
Native trees								
Species number	15	16	9	17	10	8	4	10
Individuals (n)	968	60	10	1039	9246	379	43	9668
Individuals (%)	93.2	5.8	1.0	100.0	95.6	3.9	0.4	100.0
Most abundant :								
Acer platanoides	602	28	5	**635**	4136	36	3.6	**4175**
A. pseudoplatanus	301	16	3	**320**	929	75	3.6	1007
Fraxinus excelsior	21	1.3	0.1	**23**	25	0	0	25
Quercus robur	1.2	0.1	0.2	1.5	1750	11	0	**1761**
Crataegus monogyna	0	0.1	0	0.1	1075	114	11	**1200**
Total tree species								
Species number	32	35	18	37	20	15	9	21
Individuals (n)	1259	112	23	1349	21,914	1036	1014	23,964
Individuals (%)	90.3	8.0	1.7	100	91.4	4.3	4.2	100.0
Proportion of alien species (%)	23.1	46.0	55.4	25.5	57.8	63.4	95.8	59.7

In the residential area, the most abundant species of native tree was *Acer platanoides,* of which there were twice as many individuals as of its congener *A. pseudoplatanus.* The most abundant alien species of tree was *Ailanthus altissima*, followed by *Acer negundo* and *Aesculus hippocastanum*. The total counts were generally higher for native than for alien species of trees. However, the alien *Ailanthus altissima* was the most abundant species in the tree layer (Table 6).

In the *Robinia* woods, *Acer platanoides*, again, was the most abundant native species, followed by *Quercus robur* and *Crataegus monogyna*. Yet alien species prevailed in all vegetation layers. *Robinia pseudoacacia* dominated the tree and shrub layers, but due to high seedling numbers in the herbaceous layer *Acer negundo* was even more abundant. The third among the top aliens was *Prunus serotina*.

Discussion

City scale

Our study highlights the important role of horticulture in plant invasions by repeatedly introducing and encouraging the planting of ornamentals (Dehnen-Schmutz et al. 2007, Kowarik & von der Lippe 2007). As in other cities (e.g. Chocholoušková & Pyšek 2003, Zerbe et al. 2004, Knapp et al. 2010), alien species of trees and shrubs that escape cultivation make up a major part of the alien flora of urban areas. The pronounced increase in species that escaped cultivation during the second halves of the 19th and 20th centuries (Figure 1A) coincided with important periods in Berlin's history. Berlin was named the German capital in 1871 and the subsequent urban growth was certainly associated with an increase in propagule pressure produced by the numerous newly established green spaces. In the second period new sites became available for plants to grow following bombing in World War II. Early studies report abundant populations of *Acer negundo*, *Ailanthus altissima*, *Clematis vitalba* and *Robinia pseudoacacia* in demolished areas (Scholz 1960, Kohler & Sukopp 1964). As these species were either previously absent or rare in the spontaneous flora, their post-war occurrence is a good example of the unpredictable episodic temporal variation in environmental conditions as a driver of plant invasions (Crawley 1989, Hastings et al. 2005).

Alien species of woody plants in Berlin were more likely to have come from European and western-Asian than American or eastern-Asian sources (Table 1). This result confirms those of previous studies on assemblages of alien species in urban habitats (e.g. Lososová et al. 2012). Consequently, the number of naturalized plants showed a similar geographic bias. This seems to be related to introduction history. Residence time is known to be an important predictor of plant invasions (Pyšek et al. 2009), and species from the former sources generally have been present for a longer time in central Europe and thus more likely to have escaped and naturalized than species from the latter sources (Kowarik 1995b).

The log-linear models did not reveal significant interactions among life forms and the species' status as native, escaped or naturalized (Table 2). The fact that no life form predominates in these categories may be explained by the high diversity of urban habitats, which provides suitable conditions for all the woody life forms. In contrast to other studies (Walther 2002, Walther et al. 2009), our data do not show a general increase in evergreen species over the last 200 years. The spread of some species, however, is likely to have been mediated by favourable urban climates. *Ailanthus altissima* is currently one of the most abundant species of tree in Berlin's densely built-up areas (Tables 4, 6), i.e. where urban heat island effects are strongest. Saplings of this species grow well at high temperatures in climate chambers (Kowarik & Säumel 2007, Säumel 2007). Another striking example is *Juglans regia.* Records of the cultivation of this species in Berlin date back to medieval times, but it started to spread only about 500 years later, in the 1960s (Kowarik 1995b), as it did in other regions (Loacker et al. 2007, Hetzel 2012). Determining the years of high germination revealed that milder winters enhance seedling establishment (Loacker et al. 2007).

The milder urban climate is also expected to favour native species. An exposure experiment revealed a higher percentage survival of saplings of *Acer platanoides* at inner-city sites than in the adjacent countryside following a sudden severe frost in late autumn (von der Lippe et al. 2005). Moreover, studies on urban populations of *Taxus baccata* that were descendants of park plantings suggest that November temperatures below –7.5 °C limit seedling establishment in this species (Iszkulo & Boratynski 2005). Nevertheless, the warmer urban climates obviously do not compensate totally for harsh winters. This is possibly why *Buddleja davidii* occurs at a low frequency in Berlin (Table 5) despite the strong propagule pressure generated by the numerous plantings of this species. In regions with a mild oceanic climate, this species is very abundant (Ebeling et al. 2008, Tallent-Halsell & Watt 2009, Wittig 2012).

Habitat and community scales

The log-linear models revealed a significantly higher number of alien species in urban areas than in near-natural ecosystems. This confirms the well-known general invasion pattern for species of woody plants. There are high numbers of alien species in many man-made habitats because they are subject to frequent disturbances and there is a high availability of nutrients there (Kowarik 1990b, Chytrý et al. 2008).

With the exception of *Aesculus hippocastanum*, the most common alien species of trees in Berlin (*Robinia pseudoacacia*, *Acer negundo*, *Prunus serotina, Quercus rubra, Ailanthus altissima*) are reported as invasive in other parts of Europe (e.g. Pyšek et al. 2012a) and beyond (Richardson & Rejmànek 2011). Most populations of alien species, however, do not conflict with conservation objectives in the densely built-up parts of Berlin as they are components of novel urban ecosystems that are well adapted to urban sites and contribute an array of ecosystem services (Kowarik 2011). As a consequence, *Robinia* woods in a former railway area have been included in a conservation area to allow the development of novel urban forests (Kowarik & Langer 2005).

When considering species frequency, the percentage of individual trees and shrubs that are alien does not reflect that most of the species are alien. Despite the high total species richness of alien species of woody plants, native species were found more frequently in urban areas, especially in forests. Even in the more urban habitats native species were slightly more frequent than alien species (Table 4, Fig. 1C). Studies at greater spatial scales have shown that alien species are often less frequent than native species (Hulme 2008, Knapp et al. 2009, Pyšek et al. 2012b). Our study confirms this pattern for assemblages of urban woody species at the habitat scale.

Tree counts in residential areas revealed a clear dominance of native species, but in the tree layer, the alien *Ailanthus altissima* was most abundant (Table 6). Correspondingly, the log-linear models revealed a significantly higher percentage of individuals of alien species of trees in the tree and shrub layers compared to the herbaceous layer. Prolific populations of species of native trees in the herbaceous layer might suggest a future shift to a greater dominance of native species in higher vegetation layers. As this survey assessed scattered populations of trees in residential areas that are highly fragmented and usually subject to frequent disturbances, the prevalence of alien species in the tree layer there possibly indicates that these species have a greater chance of maturing there. Other studies have found *Ailanthus altissima* to be among the most abundant species of alien tree on urban land (e.g. Pan & Bassuk 1986, Lenzin et al. 2001, Tsiotsiou & Christodoulakis 2010). Its frequent presence in the tree layer can be explained by its higher growth rate, both in shoots and roots, compared to *Acer platanoides* (Pan & Bassuk 1986, Säumel 2007). Moreover, *Ailanthus altissima* responds quickly to disturbance by regenerating vegetatively (Kowarik & Säumel 2007), which is likely to be highly advantageous in habitats subject to repeated disturbances.

The survey of the *Robinia* woods, which were about 40 years old when sampled, revealed a clear prevalence of *R. pseudoacacia* in both tree and shrub layers (Kowarik 1990a). Again, the log-linear models revealed a significantly higher percentage of individuals of alien species of trees in the tree and shrub layers compared to the herbaceous layer. The dominance of *R. pseudoacacia*, which continues today (I. Kowarik, personal observation), strongly contrasts with the development of stands of this species in its native North American range, where this pioneer tree is quickly replaced after 20–30 years by shade-tolerant native trees, mostly due to it being strongly attacked by insects (Boring & Swank 1984). The shade-tolerant native *A. platanoides* was also able to establish prolific populations in the herbaceous layer of *Robinia* woods in Berlin but as yet not in the upper vegetation layers. In contrast to early predictions (Kohler & Sukopp 1964), *R. pseudoacacia* appears to remain dominant in woods undergoing succession in its European range for longer than in its native range, possibly because it is not attacked here as much by insects as in North America.

The high frequency of native species in urban habitats (Table 4) may suggest an important potential for the recovery of native woody vegetation in urban areas (Stewart et al. 2004). Forest remnants can function as sources of propagules of native trees that colonize adjacent gardens (Doody et al. 2010) but as few parts of Berlin's built-up areas are close to forests, it is much more likely that urban trees are the major source of propagules for the recolonization by native species. This can induce biological invasions at the gene level since the horticultural sector usually provides plants grown from other than local seed sources (Petit 2004). Growth or leaf anomalies of some spontaneously occurring species of native woody plants indicates that the seeds come from particular cultivars (Ringenberg 1994, Seidling 1999) and are mainly dispersed by birds (Moller et al. 2012). Plantings in urban areas can also lead to the establishment of forest populations of native species, which mainly consist of the descendants of garden plants. This is most evident for *Acer platanoides* (Sachse 1990) but is also true for *Taxus baccata* (Seidling 1999), a native forest tree, which was extirpated in the Berlin-Brandenburg region during the 19th century (Benkert 1978). Due to the fact that all the current populations grew from seed from other provenances, *T. baccata* is currently listed as an alien species in Berlin.

Plantings of trees in urban areas have also obviously changed the abundance patterns of native species. The high abundance of *Acer platanoides* and *A. pseudoplatanus* at the habitat and community scales (Table 4, 6) is a surprising result from a historical perspective because both species were rare in Berlin up to the end of the 19th century (Ascherson

1864, Sachse et al. 1990). This pronounced increase and the invasion success of *A. platanoides* in North America can be related to frequent planting that multiplied the propagule pressure (Sachse et al. 1990, Hunter & Mattice 2002). In addition, both these species of maple respond positively to increased availability of nitrogen (Sachse et al. 1990, Pröll et al. 2011), a typical feature of many urban environments (McDonnell et al. 1997, Alberti 2005). The fact that *A. pseudoplatanus* is less frequent in urban areas in Berlin than its congener could be due to its lower tolerance of drought (Hemery et al. 2010). Overall, these results highlight that both alien and native species respond to the urban environment with converging trends at different scales.

Acknowledgements

IK was funded by BMBF (FKZ 0319304A) and all authors were supported by institutional resources of Technische Universität Berlin. We thank Petr Pyšek and three anonymous reviewers for helpful comments and Kelaine Ravdin and Tony Dixon for improving our English.

Souhrn

Invazní druhy jsou ve městech důležitou složkou květeny; k tomuto jevu významně přispívají zplaňující pěstované dřeviny. Otázkou zůstává, zda se celková druhová bohatost dřevin projevuje také na úrovni stanovišť a populací. Cílem práce je porozumět tomu, jak invaze dřevin ve městech závisejí na měřítku studia; za tímto účelem jsme analyzovali výskyt původních a nepůvodních druhů stromů keřů a popínavých dřevin spontánně se vyskytujících na území Berlína. Zastoupení nepůvodních dřevin ve flóře Berlína vzrostlo z 16 % na konci 18. století během 200 let na 67 %. Z celkového počtu 181 zaznamenaných druhů je 32 % považováno za naturalizované. Druhy z ostatních částí Evropy, z Mediteránu a západní Asie zplaněly a zdomácněly častěji než druhy z jiných oblastí. Zplaňování nezvýšilo podíl stálezelených druhů ve flóře. Všechny typy stanovišť vyjma mokřadů hostí více nepůvodních než původních druhů, procentální zastoupení nepůvodních je vysoké zejména na plochách s městskou zelení, neudržovaných místech a v obytných čtvrtích. Na úrovni stanovišť jsou však původní druhy zastoupeny relativně více. Nejčastějšími stromy bez ohledu na stanoviště jsou původní druhy *Acer platanoides*, *Betula pendula*, *Quercus robur* a nepůvodní *Robinia pseudoacacia*, *Acer negundo* a *Prunus serotina*, mezi keři pak původní *Sambucus nigra* a nepůvodní *Mahonia aquifolium*. Analýza počtu jedinců ve dvou vybraných oblastech ukázala, že původní druhy jsou početnější v obytných čtvrtích, zatímco nepůvodní v neudržovaných částech města. Výsledky potvrzují, že invazní úspěch dřevin v městském prostředí je nutno posuzovat v kontextu. Jasná převaha nepůvodních druhů v celkové flóře se nepřenáší na úroveň stanovišť a rostlinných společenstev, měřeno frekvencí výskytu. Pro městské oblasti je typické nejen vysoké zastoupení nepůvodních druhů, ale take nárůst početnosti nekterých původních dřevin, jako jsou *Acer platanoides* and *A. pseudoplatanus*, které v současnosti převládají díky zvýšenému přísunu diaspor a eutrofizaci městských ekosystémů.

References

Abendroth S., Kowarik I., Müller N. & von der Lippe M. (2012): The green colonial heritage: woody plants in parks of Bandung, Indonesia. – Landsc. Urban Plan. 106: 12–22.
Adler J. (2010): R in a nutshell. – O'Reilly Media, Köln.
Akinnifesi F. K., Sileshi G., da Costa J., de Moura E. G., da Silva R. F., Ajayi O. C., Linhares J. F. P., Akinnifesi A. I., de Araujo M. & Rodrigues M. A. I. (2010): Floristic composition and canopy structure of home-gardens in São Luís city, Maranhão State, Brazil. – J. Hort. For. 2: 72–86.
Alberti M. (2005): The effects of urban patterns on ecosystem function. – Intern. Region. Sci. Rev. 28: 168–192.
Aronson M. F. J., Handel S. N. & Clemants S. E. (2007): Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape. – Biol. Invas. 9: 465–475.
Ascherson P. (1864): Flora der Provinz Brandenburg, der Altmark und des Herzogthums Magdeburg. – Berlin.
Benkert D. (1978): Die verschollenen und vom Aussterben bedrohten Blütenpflanzen und Farne der Bezirke Potsdam, Frankfurt, Cottbus und Berlin. – Gleditschia 6: 20–59.
Bertin R. I., Manner M. E., Larrow B. F., Cantwell T. W. & Berstene E. M. (2005): Norway maple (*Acer platanoides*) and other non-native trees in urban woodlands of central Massachusetts. – J. Torr. Bot. Soc. 132: 225–235.

Bolle C. (1887): Andeutungen über die freiwillige Baum- und Strauchvegetation der Provinz Brandenburg. – Verlag des Märkischen Provinzial-Museums, Berlin.
Borgmann K. L. & Rodewald A. D. (2005): Forest restoration in urbanizing landscapes: interactions between land uses and exotic shrubs. – Rest. Ecol. 13: 334–340.
Boring L. R. & Swank W. T. (1984): The role of black locust (*Robinia pseudoacacia*) in forest succession. – J. Ecol. 72: 749–766.
Botham M. S., Rothery P., Hulme P. E., Hill M. O., Preston C. D. & Roy D. B. (2009): Do urban areas act as foci for the spread of alien plant species? An assessment of temporal trends in the UK. – Diversity Distrib. 15: 338–345.
Chocholoušková Z. & Pyšek P. (2003): Changes in composition and structure of urban flora over 120 years: a case study of the city of Plzeň. – Flora 198: 366–376.
Chytrý M., Maskell L. C., Pino J., Pyšek P., Vilà M., Font X. & Smart S. M. (2008): Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. – J. Appl. Ecol. 45: 448–458.
Crawley M. J. (1989): Chance and timing in biological invasions. – In: Drake J. A., Mooney H. A., di Castri F., Groves R. H., Kruger F. J., Rejmánek M. & Williamson M. (eds), Biological invasions: a global perspective, p. 407–423, John Wiley, New York.
Dehnen-Schmutz K., Touza J., Perrings C. & Williamson M. (2007): A century of the ornamental plant trade and its impact on invasion success. – Diversity Distrib. 13: 527–534.
Doody B. J., Sullivan J. J., Meurk C. D., Stewart G. H. & Perkins H. C. (2010): Urban realities: the contribution of residential gardens to the conservation of urban forest remnants. – Biodiv. Cons. 19: 1385–1400.
Duguay S., Eigenbrod F. & Fahrig L. (2007): Effects of surrounding urbanization on non-native flora in small forest patches. – Landsc. Ecol. 22: 589–599.
Ebeling S., Hensen I. & Auge H. (2008): *Buddleja davidii* Franch. performs better in the introduced area. – Diversity Distrib.14: 225–233.
Elssholtz J. S. (1663): Flora Marchica, sive catalogus plantarum, quae partim in hortus electoralibus Marchicae Brandenburgicae primariis, Berolinensis, Aurangiburgico, Potstamensi excoluntur: partim sua sponte passim proveniunt. – Berlin.
Elssholtz J. S. (1684): Vom Garten-Baw. Ed. 4. – Cölln.
Essl F., Milasowszky N. & Dirnböck T. (2011): Plant invasions in temperate forests: resistance or ephemeral phenomenon? – Basic Appl. Ecol. 12: 1–9.
Fitschen J. (1987): Gehölzflora. Ed. 8. [ed. Meyer F. H., Hecker U., Höster H. R. & Schroeder F.-G.]. – Heidelberg.
Franke J. (1594): Hortus Lusatiae. – Bautzen. [New edition by Zaunick R. et al. 1930, Naturwiss. Ges. Isis VI.]
Goeze E. (1916): Liste der seit dem 16. Jahrhundert bis auf die Gegenwart in die Gärten und Parks Europas eingeführten Bäume und Sträucher. – Mitt. Deutsch. Dendr. Ges. 25: 129–201.
Gregor T., Bönsel D., Starke-Ottich I. & Zizka G. (2012): Drivers of floristic change in large cities: a case study of Frankfurt/Main (Germany). – Landsc. Urban Plan. 104: 230–237.
Hastings A., Cuddington K., Davies K. F., Dugaw C. J., Elmendorf S., Freestone A., Harrison S., Holland M., Lambrinos J., Malvadkar U., Melbourne B. A., Moore K., Taylor C. & Thomson D. (2005): The spatial spread of invasions: new developments in theory and evidence. – Ecol. Lett. 8: 91–101.
Hauru S., Niemi A. & Lehvävirta S. (2012). Spatial distribution of saplings in heavily worn urban forests: implications for regeneration and management. – Urban For. Urban Green. 11: 279–289.
Hemery G. E., Clark J. R., Aldinger E., Claessens H., Malvolti M. E., O'Connor E., Raftoyannis Y., Savill P. S. & Brus R. (2010): Growing scattered broadleaved tree species in Europe in a changing climate: a review of risks and opportunities. – Forestry 83: 65–81.
Hetzel I. (2012): Ausbreitung klimasensitiver ergasiophygophytischer Gehölzsippen in urbanen Wäldern im Ruhrgebiet. – Diss. Bot. 411: 1–205.
Hulme P. E. (2008): Contrasting alien and native plant species-area relationships: the importance of spatial grain and extent. – Glob. Ecol. Biogeogr. 17: 641–647.
Hunter J. C. & Mattice J. (2002): The spread of woody exotics into the forests of a northeastern landscape, 1938–1999. – J. Torr. Bot. Soc. 129: 220–227.
Iszkulo G. & Boratynski A. (2005): Different age and spatial structure of two spontaneous subpopulations of *Taxus baccata* as a result of various intensity of colonization process. – Flora 200: 195–206.
Jim C. Y. (2000): The urban forestry programme in the heavily built-up milieu of Hong Kong. – Cities 17: 271–283.
Jim C. Y. (2008): Urban biogeographical analysis of spontaneous tree growth on stone retaining walls. – Phys. Geogr. 29: 351–373.
Jim C. Y. & Chen W. Y. (2008): Pattern and divergence of tree communities in Taipei's main urban green spaces. – Landsc. Urban Plan. 84: 312–323.

Jim C. Y. & Chen W. Y. (2011): Bioreceptivity of buildings for spontaneous arboreal flora in compact city environment. – Urban For. Urban Green. 10: 19–28.
Knapp S., Kühn I., Bakker J. P., Kleyer M., Klotz S., Ozinga W. A., Poschlod P., Thompson K., Thuiller W. & Römermann C. (2009): How species traits and affinity to urban land use control large-scale species frequency. – Diversity Distrib. 15: 533–546.
Knapp S., Kühn I., Stolle J. & Klotz S. (2010): Changes in the functional composition of a Central European urban flora over three centuries. – Persp. Plant Ecol. Evol. Syst. 12: 235–244.
Knapp S., Kühn I., Wittig R., Ozinga W. A., Poschlod P. & Klotz S. (2008): Urbanization causes shifts in species' trait state frequencies. – Preslia 80: 375–388.
Kohler A. & Sukopp H. (1964): Über die Gehölzentwicklung auf Berliner Trümmerstandorten. – Ber. Deutsch. Bot. Ges. 76: 389–406.
Kowarik I. (1990a): Some responses of flora and vegetation to urbanization in Central Europe. – In: Sukopp H., Hejny S. & Kowarik I. (eds), Urban ecology, p. 45–74, SPB Acad. Publ., The Hague.
Kowarik I. (1990b): Zur Einführung und Ausbreitung der Robinie (*Robinia pseudoacacia* L.) in Brandenburg und zur Gehölzsukzession ruderaler Robinienbestände in Berlin. – Verh. Berliner Bot. Ver. 8: 33–67.
Kowarik I. (1992): Einführung und Ausbreitung nichteinheimischer Gehölzarten in Berlin und Brandenburg und ihre Folgen für Flora und Vegetation. – Verh. Bot. Ver. Berlin Brandenburg, Beiheft 3.
Kowarik I. (1995a): 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, p. 85–103, SPB Acad. Publ., Amsterdam.
Kowarik I. (1995b): Time lags in biological invasions with regard to the success and failure of alien species. – In: Pyšek P., Prach K., Rejmánek M. & Wade M. (eds), Plant invasions – general aspects and special problems, p. 15–38, SPB Acad. Publ., Amsterdam.
Kowarik I. (2003): Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. – Biol. Invas. 5: 293–312.
Kowarik I. (2005): Urban ornamentals escaped from cultivation. – In: Gressel J. (ed.), Crop ferality and volunteerism, p. 97–121, CRC Press, Boca Raton.
Kowarik I. (2011): Novel urban ecosystems, biodiversity and conservation. – Environ. Poll. 159: 1974–1983.
Kowarik I. & Langer A. (2005): Natur-Park Südgelände: linking conservation and recreation in an abandoned railyard in Berlin. – In: Kowarik I. & Körner S. (eds), Wild urban woodlands: new perspectives for urban forestry, p. 287–299, Springer, Berlin.
Kowarik I. & Säumel I. (2007): Biological flora of Central Europe: *Ailanthus altissima* (Mill.) Swingle. – Persp. Plant Ecol. Evol. Syst. 8: 207–237.
Kowarik I. & von der Lippe M. (2007): Pathways in plant invasions. – In: Nentwig W. (ed.), Biological invasions. Ecological Studies, Vol. 193, p. 29–47, Springer, New York.
Krausch H.-D. & Sukopp H. (2010): Die Geschichte der geobotanischen Forschung in Berlin und Brandenburg. – Verh. Bot. Ver. Berlin Brandenburg, Beiheft 6: 5–155.
Křivánek M., Pyšek P. & Jarošík V. (2006): Planting history and propagule pressure as predictors of invasion by woody species in a temperate region. – Cons. Biol. 20: 1487–1498.
Kunick W. (1987): Woody vegetation in settlements. – Landsc. Urban Plan. 14: 57–78.
Lehvävirta S. (2007): Non-anthropogenic dynamic factors and regeneration of (hemi)boreal urban woodlands – synthesising urban and rural ecological knowledge. – Urban For. Urban Green. 6: 119–134.
Lehvävirta S. & Rita H. (2002): Natural regeneration of trees in urban woodlands. – J. Veg. Sci. 13: 57–66.
Lenzin H., Kohl J., Muehethaler R., Odiet M., Baumann N. & Nagel P. (2001): Verbreitung, Abundanz und Standorte ausgewählter Neophyten in der Stadt Basel (Schweiz). – Bauhinia 15: 39–56.
Loacker K., Kofler W., Pagitz K. & Oberhuber W. (2007): Spread of walnut (*Juglans regia* L.) in an Alpine valley is correlated with climate warming. – Flora 202: 70–78.
Lockwood J. L., Cassey P. & Blackburn T. (2005): The role of propagule pressure in explaining species invasions. – Trends Ecol. Evol. 20: 223–228.
Lososová Z., Chytrý M., Tichý L., Danihelka J., Fajmon K., Hájek O., Kintrová K., Kühn I., Láníková D., Otýpková Z. & Řehořek V. (2012): Native and alien floras in urban habitats: a comparison across 32 cities of central Europe. – Glob. Ecol. Biogeogr. 21: 545–555.
Lososová Z., Horsák M., Chytrý M., Čejka T., Danihelka J., Fajmon K., Hájek O., Juřičková L., Kintrová K., Láníková D., Otýpková Z., Řehořek V. & Tichý L. (2011): Diversity of central European urban biota: effects of human-made habitat types on plants and land snails. – J. Biogeogr. 38: 1152–1163.
Mack R. N. (2000): Cultivation fosters plant naturalization by reducing environmental stochasticity. – Biol. Invas. 2: 111–122.
McDonnell M. J., Pickett S. T. A., Groffman P., Bohlen P., Pouyat R. V., Zipperer W. C., Parmelee R. W., Carreiro M. M. & Medley K. (1997): Ecosystem processes along an urban-to-rural gradient. – Urban Ecosyst. 1: 21–36.

Meusel H., Jäger E. J., Rauschert S. & Weinert E. (1978): Vergleichende Chorologie der zentraleuropäischen Flora. Karten Bd. 2. – Jena.

Meusel H., Jäger E. J. & Weinert E. (1965): Vergleichende Chorologie der zentraleuropäischen Flora. Karten. – Jena.

Moller L. A., Skou A.-M. T. & Kollmann J. (2012): Dispersal limitation at the expanding range margin of an evergreen tree in urban habitats? – Urban For. Urban Green. 11: 59–64.

Mücke M. & Kliese R. (1991): Floristische und gehölzdemographische Untersuchungen des Scheunenviertels in Berlin-Mitte. – Diploma thesis, Technische Universität Berlin.

Mulvaney M. (2001): The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. – In: Groves R. H., Panetta F. D. & Virtue J. G. (eds), Weed risk assessment, p. 186–193, CISRO, Melbourne.

Nagendra H. & Gopal D. (2010): Street trees in Bangalore: density, diversity, composition and distribution. – Urban For. Urban Green. 9: 129–137.

Nagendra H. & Gopal D. (2011): Tree diversity, distribution, history and change in urban parks: studies in Bangalore, India. – Urban Ecosyst. 14: 211–223.

Neil K. L., Landrum L. & Wu J. G. (2010): Effects of urbanization on flowering phenology in the metropolitan phoenix region of USA: findings from herbarium records. – J. Arid Environ. 74: 440–444.

Niinemets U. & Peñuelas J. (2008): Gardening and urban landscaping: significant players in global change. – Trends Plant Sci. 13: 60–65.

Nowak D. J. (2012): Contrasting natural regeneration and tree planting in fourteen North American cities. – Urban For. Urb. Green. 11: 374–382.

Pan E. & Bassuk N. (1986): Establishment and distribution of *Ailanthus altissima* in the urban environment. – J. Environ. Hort. 41: 1–4.

Petit R. J. (2004): Biological invasions at the gene level. – Diversity Distrib. 10: 159–165.

Pröll G., Dullinger S., Dirnböck T., Kaiser C. & Richter A. (2011): Effects of nitrogen on tree recruitment in a temperate montane forest as analysed by measured variables and Ellenberg indicator values. – Preslia 83: 111–127.

Pyšek P. (1998): Alien and native species in Central European urban floras: a quantitative comparison. – J. Biogeogr. 25: 155–163.

Pyšek P., Chytrý M., Pergl J., Sádlo J. & Wild J. (2012a): Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. – Preslia 84: 575–629.

Pyšek P., Danihelka J., Sádlo J., Chrtek J. Jr., Chytrý M., Jarošík V., Kaplan Z., Krahulec F., Moravcová L., Pergl J., Štajerová K. & Tichý L. (2012b): Catalogue of alien plants of the Czech Republic (2nd edition): checklist update, taxonomic diversity and invasion patterns. – Preslia 84: 155–255.

Pyšek P., Křivánek M. & Jarošík J. (2009): Planting intensity, residence time, and species traits determine invasion success of alien woody species. – Ecology 90: 2734–2744.

Pyšek P. & Richardson D. M. (2007): Traits associated with invasiveness in alien plants: where do we stand? – In: Nentwig W. (ed.), Biological invasions, p. 97–125, Springer, New York.

Quinn G. P. & Keough M. J. (2003): Experimental design and data analysis for biologists. – Cambridge Univ. Press, Cambridge.

Reichard S. H. & Hamilton C. W. (1997): Predicting invasions of woody plants introduced into North America. – Cons. Biol. 11: 193–203.

Richardson D. M., Pyšek P., Rejmánek M., Barbour M. G., Panetta F. D. & West C. J. (2000): Naturalization and invasion of alien plants: concepts and definitions. – Diversity Distrib. 6: 93–107.

Richardson D. M. & Rejmánek M. (2011): Trees and shrubs as invasive alien species: a global review. – Diversity Distrib. 17: 788–809.

Ringenberg J. (1994): Analyse urbaner Gehölzbestände am Beispiel der Hamburger Wohnbebauung. – Kovac, Hamburg.

Roetzer T., Wittenzeller M., Haeckel H. & Nekovar J. (2000): Phenology in central Europe: differences and trends of spring phenophases in urban and rural areas. – Intern. J. Biometeor. 44: 60–66.

Ross C. A. & Auge H. (2008): Invasive *Mahonia* plants outgrow their native relatives. – Plant Ecol. 199: 21–31.

Sachse U., Starfinger U. & Kowarik I. (1990): Synanthropic woody species in the urban area of Berlin (West). – In: Sukopp H., Hejný S. & Kowarik I. (eds), Urban ecology, p. 233–243, SPB Acad. Publ., The Hague.

Säumel I. (2007): Temperature effects on invasive tree species: architecture, biomass allocation, plasticity and distribution patterns. – Doctoral thesis, Technische Universität Berlin.

Säumel I., Kowarik I. & Butenschön S. (2010): Green traces from past to future: the interplay of culture and ecological processes in European historical parks. – Acta Horticult. 881: 933–938.

Scholz H. (1960): Die Veränderungen in der Berliner Ruderalflora. Ein Beitrag zur jüngsten Florengeschichte. – Willdenowia 2: 379–397.

Seidling W. (1999): Spatial structures of a subspontaneous population of *Taxus baccata* saplings. – Flora 194: 439–451.
SenStadt [Senate Department for Urban Development] (2008): Berlin digital environmental atlas. Land use "06.01 Actual Use of Built-up Areas" and "06.02 Inventory of Green and Open Spaces" (edition 2008). – Senate Department for Urban Development, http://www.stadtentwicklung.berlin.de/umwelt/umweltatlas/eic601.htm. (accessed 15 June 2012).
Shustack D. P., Rodewald A. D. & Waite T. A. (2009): Springtime in the city: exotic shrubs promote earlier greenup in urban forests. – Biol. Invas. 11: 1357–1371.
Sjöman H., Östberg J. & Bühler O. (2012): Diversity and distribution of the urban tree population in ten major Nordic cities. – Urban For. Urban Green. 11: 31–39.
Stewart G. H., Ignatieva M. E., Meurk C. D. & Earl R. D. (2004): The re-emergence of indigenous forest in an urban environment, Christchurch, New Zealand. – Urban For. Urban Green. 2: 149–158.
Stewart G. H., Meurk C. D., Ignatieva M. E., Buckley H. L., Magueur A., Case B. S., Hudson M. & Parker M. (2009): Urban biotopes of Aotearoa, New Zealand (URBANZ) II: Floristics, biodiversity and conservation values of urban residential and public woodlands, Christchurch. – Urban For. Urban Green. 8: 149–162.
Sukopp H. (1987): On the history of plant geography and plant ecology in Berlin. – Englera 7: 85–103.
Sukopp H. (ed.) (1990): Stadtökologie: das Beispiel Berlin. – Dietrich Reimer Verlag, Berlin.
Sullivan J. J., Timmins S. M. & Williams P. A. (2005): Movement of exotic plants into coastal native forests from settlements in northern New Zealand. – N. Z. J. Ecol. 29: 1–10.
Tallent-Halsell N. G. & Watt M. S. (2009): The invasive *Buddleja davidii* (butterfly bush). – Bot. Rev. 75: 292–325.
The R Foundation for Statistical Computing (2012): R version 2.14.2. – http://www.r-project.org (accessed 15 July 2012).
Trentanovi G., von der Lippe M., Sitzia T., Ziechmann U., Kowarik I. & Cierjacks A. (2013): Biotic homogenization at the community scale: disentangling the roles of urbanization and plant invasion. – Diversity Distrib. (in press, doi: 10.1111/ddi.12028).
Tsiotsiou V. & Christodoulakis D. (2010): Woody plants in urban biotopes: studies in Patras (Greece). – Fresenius Environ. Bull. 19: 2958–2965.
Vidra R. L. & Shear T. H. (2008): Thinking locally for urban forest restoration: a simple method links exotic species invasion to local landscape structure. – Rest. Ecol. 16: 217–220.
von der Lippe M., Säumel I. & Kowarik I. (2005): Cities as drivers of biological invasions: the role of climate changes and traffic. – Die Erde 136: 123–143.
Walther G. R. (2002): Weakening of climatic constraints with global warming and its consequences for evergreen broad-leaved species. – Folia Geobot. 37: 129–139.
Walther G. R., Roques A., Hulme P. E., Sykes M. T., Pyšek P., Kühn I., Zobel M., Bacher S., Botta-Dukát Z., Bugmann H., Czúcz B., Dauber J., Hickler T., Jarošík V., Kenis M., Klotz S., Minchin D., Moora M., Nentwig W., Ott J., Panov V. E., Reineking B., Robinet C., Semenchenko V., Solarz W., Thuiller W., Vilà M., Vohland K. & Settele J. (2009): Alien species in a warmer world: risks and opportunities. – Trends Ecol. Evol. 24: 686–693.
Willdenow C. L. (1787): Florae berolinensis prodromus. – Berlin.
Wittig R. (2012): Frequency of *Buddleja davidii* Franch. (*Buddlejaceae*) in Germany along ecological gradients. – Flora 207: 133–140.
Woodall C. W., Nowak D. J., Liknes G. C. & Westfall J. A. (2010): Assessing the potential for urban trees to facilitate forest tree migration in the eastern United States. – For. Ecol. Manage. 259: 1447–1454.
Zacharias F. (1972). Blühphaseneintritt an Straßenbäumen (insbesondere *Tilia x euchlora* Koch) und Temperaturverteilung in Westberlin. – Doctoral thesis, Freie Universität Berlin.
Zerbe S., Choi I. K. & Kowarik I. (2004): Characteristics and habitats of non-native plant species in the city of Chonju, southern Korea. – Ecol. Res. 19: 91–98.
Zhao J., Ouyang Z., Zheng H., Zhou W., Wang X., Xu W. & Ni Y. (2010): Plant species composition in green spaces within the built-up areas of Beijing, China. – Plant Ecol. 209: 189–204.

Received 24 October 2012
Revision received 3 March 2013
Accepted 13 March 2013