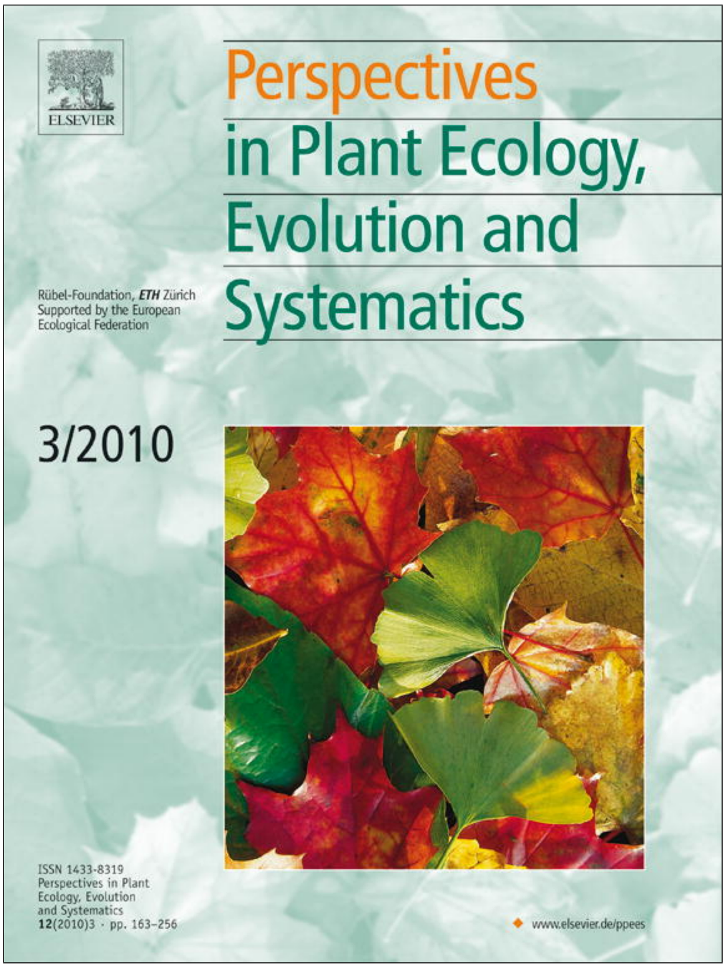

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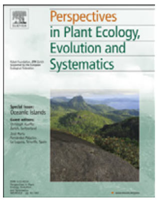

Research article

Changes in the functional composition of a Central European urban flora over three centuries

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ABSTRACT

Documents on historical floras provide unique opportunities to analyze past changes and to show trends in biodiversity. We studied the historical and recent flora of the city of Halle in Central Germany. Our earliest records date back to the year 1687; the youngest were sampled in 2008. More than 20 other floras provide information for time in-between, covering *ca.* 320 years in total. We checked all historical plant occurrences for plausibility. The species turnover of 22% that took place in the study period should also yield changes in the functional composition of the flora. We identified native species and archaeophytes that went extinct since 1689 and 1856, respectively, and all neophytes that were introduced since 1689 or 1856. This 'double' calculation minimized the influence of so-called possible pseudo-absences. Contingency tables assisted to identify trait states which were associated with extinction or introduction. Time-series analysis identified temporal trends in trait state ratio development after testing for temporal autocorrelation. Within the study period, species of bogs, nitrogen-poor habitats or plants with helomorphic leaves got extinct more often than expected by chance. Species dispersed by humans, plants preferring nitrogen-rich or warm habitats, shrubs and trees, and species with mesomorphic leaves were, amongst others, over-represented among introduced neophytes. Land-use changes such as the transformation from agriculture to urban land use or the drainage of bogs are discussed as main drivers of these developments. Additionally, climatic changes, contamination of habitats and gardeners' preferences for specific plants are presumed to having caused floristic changes. Our study shows the vast influence humans had and still have on biodiversity by intentionally or unintentionally selecting specific functional plant types and thus changing the composition of the flora.

Introduction

Urbanization has shaped European landscapes for many centuries. The first towns already developed around 700 B.C. in the Mediterranean (Antrop, 2004). Since these early times, urbanization spread all over Europe which is today highly urbanized, with 72% of the total population living in urban areas (only Latin and Northern America have higher rates of urban population with 78% and 81%, respectively; United Nations, 2006). In the 18th century and especially in the 19th century, industrialization and trade caused the growth of many European towns and cities. However, the main phase of urbanization took place in the 20th century with its rapid developments in transportation techniques (Berry, 1990; Antrop, 2004; United Nations, 2006). The increased mobility, together with other factors, such as political frameworks, enabled urban sprawl, which was especially strong in the second half of the 20th century (Kasanko et al., 2006).

Urbanization changes landscapes profoundly. In Europe, land use often changed from agricultural to urban but also from semi-natural to urban (Kasanko et al., 2006). These changes have severe impacts on climate, biogeochemical cycles, hydrology and biodiversity (Vitousek et al., 1997): compared to rural surroundings the high heat capacity of buildings together with heating increases urban temperatures (Landsberg, 1981; Oke, 1982; Sukopp, 1998); the emission of pollutants from traffic, industries and heating changes the composition of the atmosphere (Berry, 1990); decomposition rates and nitrification rates increase in urban relative to rural forest stands (McDonnell et al., 1997); the high proportion of sealed surfaces reduces infiltration capacity and groundwater replenishment (Sukopp, 1998); proportions of native species decrease, while proportions of non-native species increase (Kühn et al., 2004a; Kowarik, 2008); compositional

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similarity of species of urban regions differs from those of rural regions (Kühn and Klotz, 2006); moreover, the phylogenetic diversity of plant assemblages decreases (Knapp et al., 2008a).

It is clear from the characteristics of urban environments that not every species is able to persist there. Indeed, species with adaptations to disturbance, fragmentation, high temperature, or drought, i.e. species with traits that enable them to cope with urban conditions, are more frequent in cities than in the countryside (Wittig and Durwen, 1982; Lososová et al., 2006; Knapp et al., 2008b). Many of such differences in the functional composition of urban and rural species assemblages have been shown in space, and other studies showed that trait state composition also changes over time (Chocholoušková and Pyšek, 2003; Pyšek et al., 2004a, 2004b; van der Veken et al., 2004; Tait et al., 2005; Tamis, 2005; Lavergne et al., 2006).

We studied the development of the flora in the city of Halle in Central Germany over 320 years. The earliest available relatively complete floristic records for Halle date back to the year 1687, the most recent published records are from 2004. For the three centuries in-between, several floristic mappings are available, covering nearly the whole time-span. We are not aware of many other databases on terrestrial plants covering such a long time-span (but see Preston (2000) for Cambridgeshire and Middlesex, UK). This gives us an unique opportunity to study changes in plant species assemblages exposed to more than 300 years of urbanization. We hypothesize that changes over time reflect differences between urban and rural areas in space, with species adapted to urban characteristics increasing their proportion in the flora as urbanization intensifies.

Materials and methods

Study area

The city of Halle is situated in Central Germany, south-east of the Harz Mountains (city centre: 11°58′19″E, 51°28′59″N; Fig. 1). It covers an area of 135 km^2. With a mean annual temperature of 9 °C (range of mean monthly temperature *ca.* 0–19 °C) and an annual precipitation of 480 mm with a peak in summer, the climate is subcontinental and relatively dry, at least in the Central European context (Müller-Westermeier et al., 1999; 2001). The low precipitation is caused by the rain shadow of the Harz Mountains. Without anthropogenic influence, forests of sessile oaks (*Quercus petraea* Liebl.), hornbeam (*Carpinus betulus* L.), and lime-tree (*Tilia cordata* Mill.) would be the main zonal vegetation (Institut für Länderkunde Leipzig, 2003).

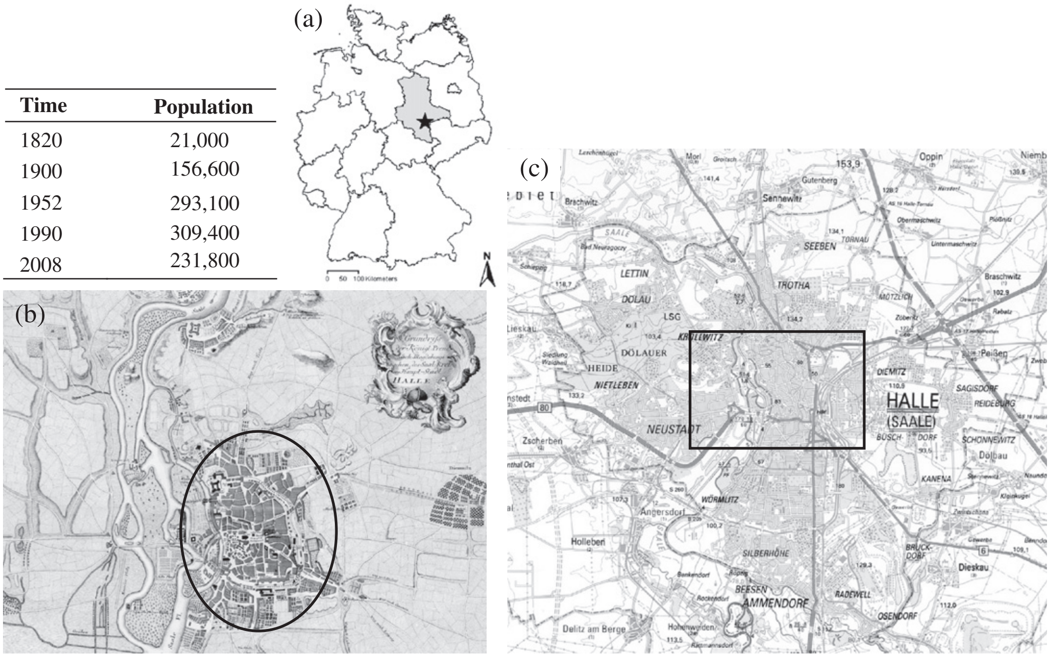
The river Saale flows through the city at an altitude of approximately 70 m a.s.l. Within the city area, the river divides in several arms, forming islands and giving room to floodplain forests. The northern part of the city is characterized by porphyric rocks that border the Saale valley. The south-western part of Halle is built on Triassic and Tertiary bedrock. The two parts are divided by a fault line, running directly through the city centre and giving rise to a salt spring from Late Permian (Wagenbreth and Steiner, 1982). The occurrence of salt was the basis for the development of Halle, besides the rich occurrences of lignite (Walossek, 2006). In the eastern part of the city area, older bedrocks are nearly completely overlaid by quaternary bedrock.

The dominant type of land-use change in our study area in the last 300 years has been urbanization, however, there are still also small agricultural and semi-natural areas left within the borders of the city. Although these are no urban habitats, they, too, have changed in the study period and are influenced by urbanization.

Data sources

Species data

We analyzed several recent and historical floras as well as smaller manuscripts with descriptions of plant occurrences of more than 18 authors and divided the data into seven time



Time	Population
1820	21,000
1900	156,600
1952	293,100
1990	309,400
2008	231,800

Fig. 1. Study area. (a) Location of the city of Halle (black star) in Central Germany, federal state Saxony-Anhalt (grey); (b) The city of Halle and its surroundings in 1740 – the circle roughly indicates the city area; (c) The city of Halle in 2002 – the rectangle shows the area of map (b). The small table shows the population development in the city with numbers from Stolle and Klotz (2004) for 1820, and http://www.halle.de (other numbers). Map (b) is the reprint of a historical city map (copper engraving attributed to Johann David Schleuen, 1740; the original copy of the map is stored in the German National Library Berlin, Preußischer Kulturbesitz.) Map (c) is the topographical map 1: 100 000 – TK 100 RK/Sheet 4 (Landesamt für Landesvermessung und Datenverarbeitung Sachsen-Anhalt, 2002).

Table 1
Overview of the time periods used in the analyses with length of the period, mean of the period used as predictor in linear models (see *Data analyses*) and respective reference floras for the region of Halle.

Time period	Mean of time period	Reference
1687–1689	1688	• Knauth, 1687, improved edition 1689
1721–1783	1752	• Buxbaum, 1721 • Senckenberg 1731, published in Spilger, 1937 • Leysser, 1761, 1783 • Roth, 1783
1806–1856	1831	• Luyken 1806 (not published but documented in the herbarium of the Westphalian Museum of Natural History in Münster) • Sprengel, 1806 • Wallroth, 1815, 1822 • Garcke, 1848, 1856
1857–1901	1879	• Fitting et al., 1899, 1901; herbarium of the University of Halle
1902–1949	1925	• Fitting et al., 1903; Schulz and Wüst, 1906, 1907; Wangerin and Ule, 1909; Knapp, 1944a, 1944b, 1945; several unpublished manuscripts by M. Schulze (1936, 1938) stored in the archive of the "working group of hercynian florists"; herbarium of the University of Halle
1950–1999	1975	• Rauschert, 1966a, 1966b, 1967, 1972, 1973, 1975, 1977a, 1977b, 1979, 1980, 1982 • several unpublished manuscripts by S. Rauschert (1959–1982) • Grosse, 1978, 1979; 1981, 1983, 1985, 1987 • Grosse and John, 1987, 1989, 1991 • Klotz, 1984 • Klotz and Stolle, 1998 • herbarium of the University of Halle
2000–2008	2004	• Stolle and Klotz, 2004 • unpublished data by J. Stolle and S. Klotz 2005–2008

Table 2
Species numbers (#) and percentages (%) of native species, archaeophytes and neophytes in the flora of Halle in seven time periods between 1687 and 2008.

Time period	# native	# archaeo	# neo	% native	% archaeo	% neo
1687–1689	599	106	6	84	15	1%
1721–1783	646	115	16	83	15	2%
1806–1856	681	122	26	82	15	3%
1857–1901	660	126	39	80	15	5%
1902–1949	633	111	49	80	14	6%
1950–1999	655	111	131	73	12	15%
2000–2008	627	102	128	73	12	15%

periods (see Table 1 for overview and references). Regarding species occurrences, we always referred to the current (2004) administrative district of Halle and not to the administrative district of the respective time periods. This was possible with the help of the site references given in the floras. Therefore, the study area today includes the city of Halle, but included the city and its immediate rural vicinity in former time periods, when the city had not yet reached today's extent.

We are aware of the fact that the floristic investigations of the 17th–19th century were not as exhaustive as today's investigations. To exclude as many uncertainties as possible, we assessed the historical floras for the plausibility of species occurrences. We excluded problematic species, i.e. species which are unlikely to have grown in the study area or species that could not be assigned to modern nomenclature. Furthermore, there are some small areas within the study area that were not recorded by the early botanists. For species with low dispersal capacities that occur in these areas today, we assumed that they also occurred there in the early times of the study period. Thus, they were included as occurring in the study area. Species occurring exclusively in cultivation were excluded.

Species which we distinguish nowadays but that were not distinguished in the past were lumped together as so-called superspecies. Therefore, we took the superspecies from the first period (1687–1689) as basis and assigned all associated species to this superspecies for all periods, also when the single species were distinguished in the following periods.

This procedure minimized inconsistencies and false occurrences as well as pseudo-absences in the floras; however, if a species was overlooked by former botanists, we do not have any evidence for its occurrence and cannot reconstruct it. This concerns native species and archaeophytes (i.e. non-native species introduced before the discovery of the Americas; Pyšek et al., 2004a, 2004b) but does not apply to neophytes (i.e. non-native species introduced after the discovery of the Americas; Pyšek et al., 2004a, 2004b), because most naturalizations of neophytes in Germany took place after 1850 (Kühn and Klotz, 2002; for Halle see Table 2) and therefore well after the first two time periods (1687–1689, 1721–1783), which have the highest probability of being inconsistent. If a species is not naturalized in Germany, it is of course not naturalized in Halle as well. We excluded casuals, i.e. neophytes that occurred only for a short time but became extinct again because their spontaneous occurrence is dependent on the occurrence of cultivated individuals or other human-dependent propagule sources. The identification of casuals was either possible with comments in the historical species lists (e.g. statements that a species only occurred in 1 year), or by likelihood: If a species was listed as occurring spontaneously in the historical lists but does not occur as an established neophyte today and is seldom cultivated (i.e. has a low propagule pressure), it was classified as a likely casual and excluded from the species list. To further account for the potential incompleteness of early floras, we performed our analyses once with the first time period as basis and a second time with the third time period as basis. Plant mapping in the third period is mainly based on Garcke (1848, 1856), whose flora is not only the most complete of the early floras but also revised faults of preceding floras (see Table 3 for species numbers per time period).

After all exclusion procedures, the first time period (1687–1689) had 820 plant species, i.e. 82% of the species numbers of the last time-span (2000–2008 with 1000 species; Table 3). Thus, the data are well representative and allow meaningful statistical analyses.

Trait data

All traits and their states (the latter being the actual parameter value or class of a categorical trait) are documented in BiolFlor, a database on biological and ecological traits of the German flora (Klotz et al., 2002; Kühn et al., 2004b; http://www.ufz.de/biolflor), except for dispersal type and specific leaf area which were taken from the LEDA database on life-history traits of the Northwest European flora (Kleyer et al., 2008; http://www.leda-traitbase.org). We chose traits related to dispersal, frost resistance, nutrient uptake, persistence, phenology, pollination, and water- and gas-exchange. These are dispersal type, flowering phenology, leaf anatomy, leaf persistence, life form, life span, pollination type, and specific leaf area (SLA). As leaf anatomy is related to the species' gas- and water-exchange, the trait includes some root characteristics, such as whether there is aeration tissue in the roots (for this and all other trait definitions see the homepages of BiolFlor and LEDA). Furthermore, we chose Ellenberg indicator values that

Table 3
Number (#) of plant species, extinct native and archaeophyte species and newly occurring neophytes in the Halle region per time period.

Time period	# plant species	# extinct natives	# extinct archaeophytes	# introduced neophytes
1687–1689	820	–	–	–
1721–1783	904	5	–	10
1806–1856	966	13	1	12
1857–1901	956	31	2	14
1902–1949	918	50	13	14
1950–1999	1045	27	3	83
2000–2008	1000	19	4	1

Numbers of extinctions and introductions are not shown for 1687–1689, because this is the reference period (see Materials and Methods). Differences in the number of species between the periods deviate from the sum of extinctions and introductions because not only the neophytes shown here were introduced but also natives and archaeophytes (not shown).

Table 4
β_{sim}-similarity index comparing the presence and absence of plant species between pairs of time periods for the flora of Halle. β_{sim} is calculated as $\beta_{sim}=a/(a+\min(b, c))$, where a is the number of species shared between two periods and b and c are the numbers of species unique to a period.

	1687–1689	1721–1783	1806–1856	1857–1901	1902–1949	1950–1999
1687–1689						
1721–1783	0.97					
1806–1856	0.96	0.94				
1857–1901	0.93	0.90	0.93			
1902–1949	0.84	0.81	0.88	0.92		
1950–1999	0.81	0.80	0.81	0.84	0.95	
2000–2008	0.78	0.76	0.77	0.80	0.91	0.99

Values range from zero to one with the upper limit indicating complete similarity and the lower limit indicating no similarity between the species lists of two periods.

reflect the plants' preferences for local moisture regime, temperature regime and nitrogen content. Ellenberg values are species-specific scores ranging from 1 to 9 (or 1 to 12 for moisture). They estimate the optimum ecological occurrence of species along environmental gradients, considering competition between species and reflecting habitat conditions, i.e. they reflect the realized niche position of a species (Ellenberg et al., 2001). The floristic status of a species (whether it is native, archaeophyte or neophyte in Germany as recorded in BiolFlor) was used to distinguish between extinctions and introductions.

Ellenberg values and floristic status are no real species traits (Violle et al., 2007); however, we call them traits here for simplicity.

Data analyses

Change of trait states with time

We first calculated the number of species per trait state and time period. χ^2-tests or Fisher's exact tests, respectively, showed whether trait states differed across time spans. Fisher's exact test had to be used if the number of at least one of the expected elements per time period was <5 (Crawley, 2007). Because changes in trait state numbers might become clearer when only comparing the first and last time period, we repeated the analyses for 1687–1689 and 2000–2008.

Association of trait states with extinction and introduction

Additionally, we calculated the number of species per trait state for (i) all native plant species extinct after 1689, (ii) all archaeophytes extinct after 1689, and (iii) for all neophytes that were introduced since 1689. We tested for associations of trait states with extinction or introduction by comparing species numbers of trait states in the basis period (1687–1689) with the species numbers of (i), (ii) and (iii) using χ^2-test or Fisher's exact test, respectively. For comparison with extinct natives (i) we referred to all natives present in the reference period; for extinct archaeophytes (ii) we referred to all archaeophytes present in the reference period; and for introduced neophytes (iii) we referred to all species present in the reference period (i.e. natives, archaeophytes and neophytes). To exclude patterns that might occur because of incomplete mapping in 1687–1689, we repeated these calculations with the third time period (1806–1856) as reference period.

Trends in the development of trait state ratios

χ^2-test and Fisher's exact test are based on species numbers, not on species proportions per time-span. However, the proportion of one trait state to another gives more detailed information about compositional changes of the flora: The number of species with a certain trait state can increase, but at the same time, the proportion of this trait state in the flora can decrease, if another state of the same trait increases even more strongly. Because the different states of a trait add up to 100%, they are not independent from each other. To break this unit sum constraint, we calculated log-ratios of proportions (Aitchison, 1982; Elston et al., 1996; Billheimer et al., 2001; Kühn et al., 2006), i.e. the log-transformed ratio of one trait state over another, e.g. the ratio of zoochorous species to anemochorous species. The choice of the denominator is irrelevant in this method.

First, we tested the log-ratios for temporal autocorrelation. Temporal autocorrelation occurs because the flora of a time period partly depends on the flora of the preceding time period, i.e. the species pool of period A is the basis for the species pool of period B (Zobel, 1997). This is illustrated by species turnover, which increases with increasing temporal distance between periods (Table 4). However, none of the log-ratios in our analysis was significantly autocorrelated in time (not shown); thus, there was no need to account for temporal autocorrelation in the linear models. We used simple linear models with the log-ratios as response and the mean of each time period as predictor and tested whether there is a significant positive or negative trend for the development of trait state ratios over time (Crawley, 2007). Here, we considered the total flora per time period, not only extinct or introduced species. We used the mean of each time period (e.g. 1688 for 1678–1689; see Table 1) to account for the different lengths of time-lags in-between the periods.

All calculations were performed with the open source software R, version 2.6.0 (R Development Core Team, 2007).

Results

Changes of trait states with time

Only life form changed significantly ($p<0.05$) over time when comparing species numbers per trait state for all time periods.

Comparing only the first and the last time period showed changes for Ellenberg moisture, Ellenberg nitrogen, leaf anatomy (all with $p<0.05$), and life form ($p<0.01$): species of dry to fresh soils, species of inundated soils and aquatic species increased in numbers between 1687–1689 and 2000–2008, while species of moist to wet soils (among them many species growing in bogs) decreased. Species of nitrogen-poor habitats decreased, and species preferring medium nitrogen contents or nitrogen-rich habitats increased. Helomorphic species (adapted to lack of

Table 5
Significance of the association of plant trait states with extinct natives ($P_{\text{extinct natives}}$); extinct archaeophytes ($P_{\text{extinct archaeophytes}}$) and introduced neophytes ($P_{\text{introduced neophytes}}$) in the flora of Halle (p-values from χ^2-test or Fisher's exact test, respectively).

Traits	$P_{\text{extinct natives}}$	$P_{\text{extinct archaeophytes}}$	$P_{\text{introduced neophytes}}$
Dispersal type	> 0.1 n.s	> 0.1 n.s	$< 0.01^{**}$
Ellenberg moisture	$< 0.01^{**}$	> 0.1 n.s	> 0.1 n.s
Ellenberg nitrogen	> 0.1 n.s	> 0.1 n.s	$< 0.001^{***}$
Ellenberg temperature	$< 0.01^{**}$	< 0.1 +	$< 0.001^{***}$
Flowering phenology	> 0.1 n.s	> 0.1 n.s	> 0.1 n.s
Leaf anatomy	$< 0.01^{**}$	> 0.1 n.s	$< 0.001^{***}$
Leaf persistence	$> 0.05^{*}$	> 0.1 n.s	< 0.1 +
Life form	> 0.1 n.s	> 0.1 n.s	$< 0.001^{***}$
Life span	> 0.1 n.s	> 0.1 n.s	> 0.1 n.s
Pollination type	> 0.1 n.s	> 0.1 n.s	< 0.1 +
Specific leaf area	> 0.1 n.s	> 0.1 n.s	> 0.1 n.s

Shown is the association in comparison with (i) native species present in 1687–1689 (for natives), (ii) archaeophytes present in 1687–1689 (for archaeophytes) and (iii) natives, archaeophytes and neophytes present in 1687–1689 (for neophytes). $p \geq 0.1$ n.s., $0.1 > p > 0.05$+; $p \leq 0.05^{*}$; $p \leq 0.01^{**}$, $p \leq 0.001^{***}$.

oxygen in swampy soils) decreased their numbers, and species with mesomorphic or hygromorphic leaves increased their numbers. The number of hemicryptophytes decreased, while the number of phanerophytes increased.

Association of trait states with extinction and introduction

Using the first time period as basis for comparison with extinct and introduced species mostly yielded the same results as using the third time period. Therefore, the following results apply to both calculations, except where indicated otherwise. For numbers of extinct and introduced species per time period see Table 3.

Introduced neophytes were more often dispersed by humans but less often by wind than expected in the reference period (Table 5, illustrated with proportions in Fig. 2a). Native species of moist to wet soils, e.g. plants growing in bogs, got preferably extinct, while species preferring drier soils were less often extinct than expected (Table 5, Fig. 2b). Also native species preferably growing in nitrogen-poor soils were marginally associated with

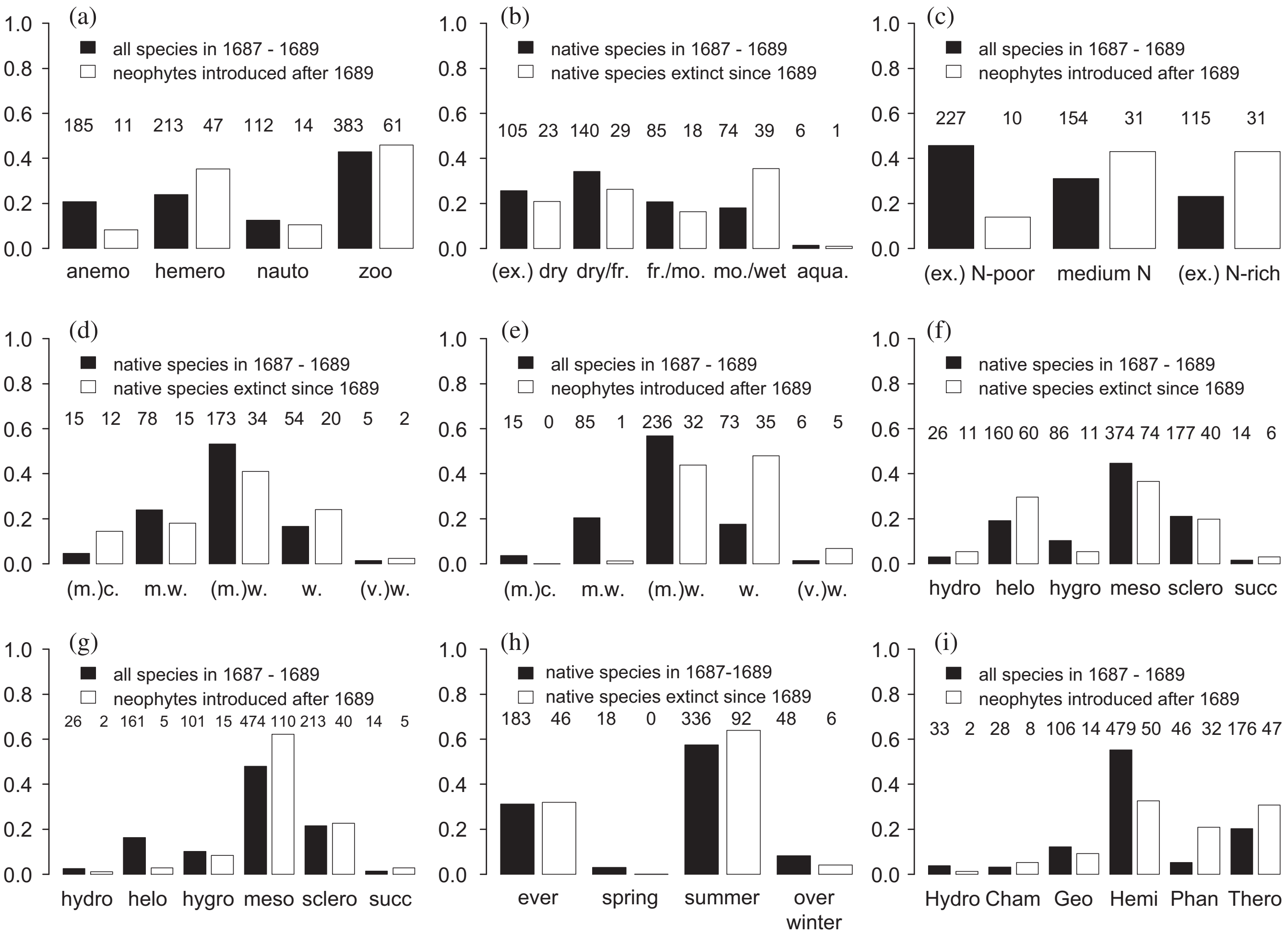


Fig. 2. Association of plant trait states with native species extinct and neophytes introduced after 1689 (until 2008) in the flora of Halle. Shown are all significant results with $p < 0.05$ from Table 5. The bars represent the proportion of each trait state (range: 0.0–1.0 = 0–100%) in the respective flora: If association with extinct native species is shown, the reference flora consists of all native species present in 1687–1689. If association with newly occurring neophytes is shown, the reference flora consists of all species (native, archaeophyte, neophyte) present in 1687–1689. The numbers over the bars represent the respective number of species. (a) dispersal type with anemo = anemochorous, hemero = hemerochorous, nauto = nauto-/hydrochorous, zoo = zoochorous; (b) Ellenberg moisture values with ex. = extremely, fr. = fresh, mo. = moist, aqua. = inundated/aquatic; (c) Ellenberg nitrogen values with ex. = extremely; (d) Ellenberg temperature values, extinctions with m. = moderately, c. = cool, w. = warm, v. = very; (e) Ellenberg temperature values, introductions (abbreviations see (d)); (f) leaf anatomy, extinctions with hydro = hydromorphic, helo = helomorphic, hygro = hygromorphic, meso = mesomorphic, sclero = scleromorphic; (g) leaf anatomy, introductions (abbreviations see (f)); (h) leaf persistence; (i) life form with Hydro = hydrophyte, Cham = chamaephyte, Geo = geophyte, Hemi = hemicryptophyte, Phan = phanerophyte, Thero = therophyte.

Table 6
Trends of trait state ratios (log-transformed with base e; see *Data analyses*) over the study period for the flora of Halle.

Trait	Log-ratio	Estimate	T	R^2_{model}
Dispersal type	Hemerochory/anemochory	0.60***	+	0.89***
	Nautochory/anemochory	−0.01 n.s		−0.2 n.s
	Zoochory/anemochory	0.39***	+	0.9***
Ellenberg moisture	2–3/10–12	−1.00*	−	0.56*
	4–5/10–12	−0.50 n.s		0.16 n.s
	6–7/10–12	−0.70 n.s		0.29 n.s
	8–9/10–12	−2.70**	−	0.83**
Ellenberg nitrogen	1–3/7–9	−1.00***	−	0.9***
	4–6/7–9	0.00 n.s		−0.2 n.s
Ellenberg temperature	3–4/8	−3.00**	−	0.79**
	5/8	−0.70 n.s		0.19 n.s
	6/8	−1.00*	−	0.61*
	7/8	−0.54 n.s		0.26 n.s
Flowering phenology	Pre-spring/early autumn	0.10 n.s		−0.16 n.s
	Early spring/early autumn	−0.80*	−	0.57*
	Mid spring/early autumn	−1.00**	−	0.79**
	Early summer/early autumn	−1.00*	−	0.62*
	Midsummer/early autumn	−1.00*	−	0.64*
Leaf anatomy	Helomorphic/hygromorphic	−2.00**	−	0.82**
	Hydromorphic/hygromorphic	−1.00 +	−	0.38 +
	Mesomorphic/hygromorphic	−0.30 n.s		0.18 n.s
	Scleromorphic/hygromorphic	−0.70*	−	0.68*
	Succulent/hygromorphic	−1.00 +	−	0.46
Leaf persistence	Evergreen/overwintering green	0.20 n.s		−0.02 n.s
	Spring-green/overwintering green	1.00*	+	0.57*
	Summer green/overwintering green	0.20 n.s		−0.04 n.s
Life form	Hydrophytes/therophytes	−0.30 n.s		0.004 n.s
	Chamaephytes/therophytes	0.40 n.s		0.04
	Geophytes/therophytes	0.06 n.s		−0.19 n.s
	Hemicryptophytes/therophytes	−0.20 n.s		−0.06 n.s
	Phanerophytes/therophytes	2.00*	+	0.62*
Life span	Annuals/biennials	−0.20 n.s		−0.06 n.s
	Pluriennials/biennials	−0.07 n.s		−0.17 n.s
Pollination type	Insect/wind	0.30 +	+	0.46 +
	Self/wind	0.20**	+	0.74**
Specific leaf area	$\mathrm{SLA} < 20\ \mathrm{mm^2/mg/SLA} > 60\ \mathrm{mm^2/mg}$	0.04 n.s		−0.2 n.s
	$20\ \mathrm{mm^2/mg} < \mathrm{SLA} < 40\ \mathrm{mm^2/mg/SLA} > 60\ \mathrm{mm^2/mg}$	0.09 n.s		−0.2 n.s
	$40\ \mathrm{mm^2/mg} < \mathrm{SLA} < 60\ \mathrm{mm^2/mg/SLA} > 60\ \mathrm{mm^2/mg}$	0.20 n.s		−0.17 n.s

Shown are parameter estimates of linear trend models (given in thousandths per year) with their error probability and model R^2 (adjusted for number of predictors) with its error probability. T (trend) indicates whether the trend over time, as shown by the parameter estimate, is positive (+) or negative (−). $p \geq 0.1$ n.s., $0.1 > p > 0.05$ +; $p \leq 0.05$*; $p \leq 0.01$**, $p \leq 0.001$***.

extinction, but only with the third time period as reference period. Furthermore, neophytes occurred less often than expected when preferring low nitrogen contents, but more often when preferring high nitrogen contents (Table 5, Fig. 2c). Native species of (moderately) cool habitats and natives and archaeophytes of warm habitats went extinct more often than expected. However, at the same time, neophytes preferring warm habitats occurred more often than expected (Table 5, Fig. 2d, e). Helomorphic native species were especially prone to extinction, and helomorphic neophytes appeared less often than expected. Moreover, hygromorphic and mesomorphic natives went extinct less often than expected and newly occurring neophytes were most often mesomorphic (Table 5, Fig. 2f, g). Concerning leaf persistence, none of the native species extinct after 1689 was spring-green and also plants with overwintering leaves went extinct less often than expected. Contrarily, summer green leaves were over-represented among extinct natives (Table 5, Fig. 2h). Phanerophytes and therophytes were over-represented among newly occurring neophytes, while other life forms, such as hydrophytes or hemicryptophytes were under-represented (Table 5, Fig. 2i). Lastly, flowering phenology, life span and specific leaf area were neither associated with extinction nor introduction (Table 5; see here for marginally and non-significant results as well).

Trends in the development of trait state ratios

The trend analyses mainly confirmed the tests for association with extinction and introduction (see Table 6 for all trends of trait state ratios). Additionally, the proportions of animal-dispersed species increased from 1687 to 2008, at the expense of wind-dispersed species. Species of inundated soils and aquatic species increased their proportion at the expense of species preferring (extremely) dry soils or moist to wet soils. Species that flower in pre-spring were the only phenological group that did not decrease in proportion. All others decreased due to the increase of species flowering in early autumn. The proportions of therophytes decreased, but only relative to phanerophytes, which increased their proportions in the flora of Halle. Insect- and self-pollinated species increased their proportions at the expense of wind-pollinated species.

Discussion

Historical data of course are associated with uncertainties. Incomplete mappings that cannot be completed several hundred years later can give a wrong picture of former floras. Our dataset, however, is reliable enough to give representative results for several reasons: Firstly, botany has a long tradition in the Halle region where Johannes Thal in 1577 wrote the first known flora worldwide (Rauschert, 1977a) that did not only concentrate on pharmaceutical or agricultural plants but included as many plant species as possible and covered a complete region (Thal, 1588; published in reprint in 1977). Many others followed, building on Thal's knowledge and passing it to others. Secondly, with 820 species in 1687–1689 and 1000 species in 2000–2008, the representativeness of the earliest flora is already high. Thirdly, we minimized uncertainties by checking the dataset for unlikely occurrences (an example is *Carex limosa* L.; two of us, J.S. and St.K., are experienced botanists who have studied the flora of Halle intensely for many years), and by taking natives and archaeophytes mapped in the first (resp. third) time period as basis. Comparing all species occurring in the reference time period with all species occurring today increases the influence of pseudo-absences. Looking only at those natives and archaeophytes that disappeared since the reference time period circumvents the problem of pseudo-absences. Fourthly, the flora of the third time period is known to be thoroughly mapped and taking this period as basis for comparison mostly yielded the same results as taking the first time period as basis. Lastly, our study revealed several patterns that are expected, self-evident or in line with other studies, such as the increase of human-dispersed species and the increase of species of nitrogen-rich habitats (Preston, 2000; Godefroid, 2001; Tamis, 2005; Römermann et al., 2008).

Urbanization is not the only type of land use that has changed European landscapes in the last centuries. Comparing both the floristic changes in the Halle area and a neighbored, e.g. agricultural, area would give a more complete picture of land-use induced floristic changes. However, as such data are not available we concentrate on changes in the urban area of Halle.

Urbanization has changed the face of the study area considerably. Halle transformed from a small town in the borders of a city wall in the 17th century to a modern city (Fig. 1) that forms, together with the neighboring city of Leipzig, the tenth largest conurbation in Germany (Friedrich, 2006). The process of urbanization caused a considerable species turnover of 22% in 320 years with the major changes occurring in the 20th century. Consequently, the changes in the proportions of trait states that we observed in our analysis are likely to reflect the change in land use and the accompanying environmental changes. However, it has to be clearly stated that urbanization is not the only driver of floristic changes; other types of land-use change as well as climate change do cause floristic changes, too. Accordingly, some of the developments in the functional composition of the flora are also known for non-urban regions: This is especially true for nitrogen inputs in Europe that increased drastically since the advent of modern agricultural techniques, industries, and traffic (Franzaring and Fangmeier, 2006), leading to a general increase in the proportion of plant species that grow in nitrogen-rich habitats and a reduction of habitats for plant species that prefer nitrogen-poor conditions (Tamis, 2005; Römermann et al., 2008).

Similarly, the increase in the proportion of plant species preferring warm habitats (Fig. 2e) is not restricted to urbanized areas (Tamis, 2005). Urban temperatures exceed temperatures of non-urban areas (Landsberg, 1981; Oke, 1982; Sukopp, 1998), but climate change has increased temperatures of both urban and rural areas (Intergovernmental Panel on Climate Change, 2007; http://www.ipcc.ch). However, many neophytes with an origin in warmer climates perform especially well in cities because urban winter temperatures allow them to persist there (Sukopp et al., 1979). Thus, the increase of heat preferring plants might be especially high in urban areas which are pre-adapted to the anticipated potential developments under climate warming.

Changes in temperature also cause phenological changes (e.g. Roetzer et al., 2000; Badeck et al., 2004; Menzel et al., 2006). Flowering as well as leaf phenology in the study area showed changes at the beginning and end of the vegetation period (Table 6, Fig. 2h), indicating an increase of temperature and in the length of the vegetation period in the Halle region over the last three centuries, probably due to both the urban heat island and climate change: Flowering starts earlier and stops later, and proportions of plant species with spring-green leaves increased. An earlier onset of the growing season was also observed for non-urban floras (European shrubland species; Prieto et al., 2009).

Besides, gardeners' preferences might influence phenological patterns: Plants flowering in pre-spring (such as *Galanthus nivalis* L.) or autumn (such as *Solidago canadensis* L.) are attractive for gardening, because many gardeners want their gardens to be green and flowering as long as possible. Similarly, insect-pollinated plants often have showy flowers and are more attractive than many wind-pollinated species. Shrubs and trees (phanerophytes) are planted along roads or in parks, among them also neophytes such as *Ailanthus altissima* (Mill.) Swingle or *Robinia pseudoacacia* L. (Kowarik and Säumel, 2007), increasing species numbers of shrubs and trees in the urban flora. Hanspach et al. (2008) showed that gardening supports the naturalization of alien plant species: The higher the number of Botanic Gardens in which a species is planted, the higher is the species' propagule pressure and the higher its probability of naturalization.

Because many neophytes reach their 'new home' with trade and traffic (Hulme, 2009), it is a logical consequence that the proportion of plant species known to be dispersed by humans in the flora of Halle increased over time (Table 6, Fig. 2a), but also animal-dispersed species seem to have profited from urbanization. First, domestic animals like cats and dogs are very frequent in urbanized areas and potential dispersers of plant seeds. Secondly, epizoochorous species, i.e. plant species with adhesive dispersal, might not only be dispersed by animals but also by humans and vehicles (Hodkinson and Thompson, 1997; von der Lippe and Kowarik, 2007; 2008) – there might be many species that can be dispersed by humans, but that are classified otherwise because their ability to use humans as dispersal vectors is not known. In this vein, Fischer et al. (1996) found that e.g. sheep disperse many more species' seeds in their fleece than considered to be genuine "epizoochoric". Additionally, species with fleshy fruits, being dispersed after digestion, are as well attractive to gardeners, if fruits are colored and showy. There are many birds in cities that disperse fleshy fruits. The decrease in the percentage of wind-dispersed species (Table 6, Fig. 2a) might be due to unsuitable conditions in urban areas, where calms are more frequent than in the countryside (Kuttler, 1993) and seeds do not reach the lee of walls and houses. However, Lososová et al. (2006) found wind-dispersed species to be more frequent in urban than in agricultural habitats and assigned this pattern to the fragmentation and dynamic nature of urban landscapes. Moreover, there is an increase of air turbulences over urban areas that should enhance the presence of wind-dispersed species. Consequently, our result might also be an artifact, due to the increase in other dispersal types. However, the decreased percentage of wind-dispersed species might also be caused by gardeners' preferences: They might be introduced less often because they are less attractive for planting than animal-dispersed species with fruits or cones.

The decrease of agricultural land use and the increase of urban land use in the study area are also likely to have increased the proportion of plants with hygromorphic leaves (Table 6), which are sensitive to drought: arable fields in the study area were mostly open, sunny habitats, but gardens, parks, and cemeteries are often shady, providing habitats less susceptible to drought, e.g. under stands of trees. The decrease of plants with hydromorphic leaves (Fig. 2f, g) might be a result of industrial contamination of water bodies.

Surprisingly, species that grow preferably on inundated soils and aquatic plants increased their relative proportion in the flora of Halle (Table 6), although the river Saale that runs through the city, a main habitat for aquatic plants, was polluted for a long time: It served as the city's discharge system for untreated wastewater (until a sewage treatment plant was built in 1915) and it was biologically dead in the 1970ies and 1980ies when wastewater from the chemical industry south of Halle but also wastes from lignite and potash mining polluted the water (Stolle and Klotz, 2004; Walossek et al., 2006). The increase in the percentage of aquatic plant species is probably due to introduced neophytes such as *Azolla filiculoides* Lam. or *Elodea canadensis* Michx. The pool of aquatic species in the study area is not very large (seven species in the first time period, 10 species in the last time period). Thus, a small number of neophytes can already increase relative proportions of aquatic species. Furthermore, several open pits from lignite mining in the city area were flooded after the end of usage and increased the available habitat for aquatic species. Earlier, the drainage of bogs for coal mining probably caused the extinction of many plants growing in bogs (e.g. *Drosera rotundifolia* L., *Eriophorum angustifolium* Honck. or *Orchis palustris* Jacq.). This corresponds to the loss of species from nitrogen-poor habitats and the loss of helomorphic species, whose roots with aeration tissue allow them to grow in swampy, oxygen-poor soils.

The proportions of life span types and categories of specific leaf area (see Table 6) were stable between 1687 and 2008. Therefore, being annual, biennial or pluriennial or having a certain SLA seems to be less susceptible to changes in land use or other environmental changes. However, it might as well be that these traits are similarly influenced by urban and agricultural land use, which both put strong disturbances on vegetation: Land use in the Halle region mainly changed from agricultural to urban, and agriculture might have affected the SLA of species long before urbanization did.

Many of the changes in the functional composition of the flora of Halle that took place in the last 320 years can also be observed in space when comparing recent urban and rural floras: Human-dispersed and animal-dispersed species, neophytes and therophytes are more frequent in urban than in rural areas in Germany (Knapp et al., 2008b). However, insect-pollinated plants and species with hygromorphic leaves seem to be less frequent in urban than in rural areas (Lososová et al., 2006; Knapp et al., 2008b), in contrast to the increase of these species in Halle over time. The relation between species richness and human presence changes with scale (Pautasso, 2007) and scaling is an important issue in analyzing trait compositions. Differences in scale yielded hence different results in trait compositions of alien vs. native species in Germany (Küster et al., 2010). Lososová et al. (2006) worked with plots $\leq 100\,\mathrm{m}^2$; Knapp et al. (2008b) investigated grid-cells sized *ca.* 130 km^2. Studies working at the scale of single cities and their surroundings found patterns similar to our temporal patterns: Wittig and Durwen (1982) for example found more species preferring nitrogen-rich, dry, warm habitats in cities in the West of Germany. Differences between spatial studies and our temporal analysis might also be due to the fact that other land-use types changed as well in the last 320 years: Agricultural intensification is only one example. Therefore, comparing an area formerly dominated by agriculture and today by urban land use, such as the Halle area, does not necessarily reflect differences between today's agricultural and urban areas. A parallel temporal analysis of floristic changes in an agricultural area would complete the picture and also help to identify which of the changes we observed are purely driven by urbanization, and which are due to not exclusively urban parameters, such as the general increase in the use of fertilizers, or climate change.

Our study shows the vast changes in an urban flora caused by the influence humans had and still have on biodiversity by intentionally (gardeners preferences) or unintentionally (changing environmental conditions) selecting specific functional plant types and thus changing the composition of the flora. Despite uncertainties, historical floras provide unique opportunities to analyze past changes in biodiversity and to show trends that might proceed in the future.

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