



# Functional diversity changes in native and alien urban flora over three centuries

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**Abstract** Alien species in urban areas have a large effect on overall species diversity. A suitable metric of flora's response to environmental change is functional diversity (FD) that refers to the multivariate space of species' trait compositions, reflecting their ecological niches. We studied how FD changed over 320 years of urbanization in the city of Halle (Saale), Germany. Selected functional traits (related to stress-tolerance, reproduction, competitiveness and phenology) were examined for the difference in FD between native and alien plant species, the latter specifically for archaeophytes, neophytes and invasive species. Functional diversity for each trait was calculated using Rao's Q index followed by a linear model to test for changes in Rao's Q over time between the groups. Over the

320 years, overall FD remained constant despite species turnover, but FD significantly increased for neophytes and invasive species compared to native species. Plant height was the only trait showing increase in FD as main effect, while for the other traits examined FD decreased over time. Considering invasive species separately, the majority of traits exhibit a significant increase in FD except for seed mass where it decreased. Finally, FD of multiple functional traits combined decreased over time. This can be due to homogenization of functional trait between native and alien species, as a consequence of habitats becoming more similar and subsequent habitat filtering. Our results demonstrate that during the last three centuries, urbanization influenced plant FD in various ways and may contribute to future uniformity of urban floras and greater invasiveness.

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## Introduction

“There was no doubt about it: the City was the culmination of man’s mastery over the environment”, Isaac Asimov wrote in his 1953 novel *The Caves of Steel*. The major factors behind the changes in species composition are human activities, particularly as their settlements expand and many habitats change or disappear. Processes associated with urbanization are mainly related to human population growth and increased area of infrastructure built for living, industry, and traffic (Sukopp 2008; Hua et al. 2017). These, further lead to habitat loss and fragmentation (Kowarik 1995a; Syphard et al. 2011), pollution, changes in climate (temperature, moisture), hydrological systems (Paul and Meyer 2001), and soil (Kalnay and Cai 2003; Trusilova et al. 2008; Song et al. 2014). Urbanization leads to habitats becoming more homogenized and thus many specialist species get lost (loss of natural or specific anthropogenic habitats) to the benefit of generalists and species adapted to urban conditions (Williams et al. 2015). In parallel, species mobility (dispersal ability) plays an important factor in colonizing new urban habitats (Concepción et al. 2015), where those species that are highly mobile respond positively to increases in the proportion of urban habitats. Additionally, alien plant species are very abundant in cities, to which they were mostly deliberately introduced, and these urban and suburban areas provide a range of different local conditions suitable for a variety of species (Lippe and Kowarik 2008). Humans benefit from urban plant species that provide multiple ecosystem services in cities, such as air quality improvement, noise reduction (Bolund and Hunhammar 1999), climate regulation, water regulation and storage, aesthetics and recreation (Gómez-Baggethun and Barton 2013; Potgieter et al. 2017) or food provision (via urban gardening; Barthel et al. 2014). Further, those alien species that become invasive can impact ecosystem services and disservices by affecting local diversity, causing health issues (i.e. allergic reactions) or damaging infrastructure (Shackleton et al. 2018; Vaz et al. 2017).

Biodiversity has been widely studied using many different measures, such as species abundance and species richness (Díaz et al. 2006). However, these measures might not be the most appropriate proxy to determine the effect of biodiversity on ecosystem processes (and vice versa). For example, studying the effect of species abundance on ecosystem processes may divert from the possible impact rare species might have on ecosystem functioning. Further, not only total species richness but also the number of species responding differently to environmental changes is crucial for understanding ecosystem processes. To this end, taking into account species’ functional traits via calculating functional diversity (FD) is considered to be more appropriate (Mcgill et al. 2006; Villéger et al. 2008). Functional diversity accounts for “the range and value of those species and organismal traits that influence ecosystem functioning” (Tilman 2001) and several FD indices relate this to the distribution of species in niche space (e.g. functional richness, evenness, divergence; Mason et al. 2005). Additionally, specific functional traits of plant species can explain different ecosystem processes. For example, leaf traits can be related to drought tolerance and competition, seed traits to life strategies, dispersal and establishment, and root traits or species height help in understanding invasibility and community competitiveness (Laughlin 2014; Funk et al. 2017). Further, SLA (specific leaf area) underlines strategies of nutrient acquisition and competition, while pollination type and flowering period relate to species dispersal. Using functional traits (rather than only species richness or abundance) is therefore particularly important in communities with an abundance of alien and invasive species because higher FD indicates a higher resistance to invasion (Funk et al. 2008).

The numbers of alien plant species introduced into Europe steadily rose from the fifteenth century with a more intensive increase in the nineteenth century (Pyšek et al. 2009). Many of them have been introduced to cities due to their prospective provision of ecosystem services, and since then, many have spread into natural areas where they modify ecosystem properties (Potgieter et al. 2019). Additionally, it is expected that alien plant invasions will intensify in the future depending on socioeconomic scenarios (particularly in arable and urban landscapes; Chytrý et al. 2012), and due to the phenomenon of invasion debt (Essl et al. 2011). Thus, having a record of invasive

species through time (decades or centuries) presents a unique opportunity and can be important for studying invasiveness and assessing future trends. So far, comparisons of historical urban floras with the present state were made for Leipzig (1867–1989 Klotz and Gutte 1992; Scholz 2008), Halle/Saale (1848–1983, Klotz 1984; 1687–2005, Knapp et al. 2010), Zürich (1839–1998, Landolt 2000), Plzeň (1880–1990s Chocholoušková and Pyšek 2003; Pyšek et al. 2004a), Brussels (Godefroid 2001), Turnhout (Van der Veken et al. 2004), Bologna (1894–2018, Salinitro et al. 2019), New York City (DeCandido et al. 2004), Indianapolis (Dolan et al. 2011), and Adelaide (Tait et al. 2005), as well as for selected parts of a city (e.g. Pelham Bay Park, New York City (DeCandido 2004), Central Park New York City (DeCandido et al. 2007)). Still, none of these studies focused on functional diversity.

In our paper, we followed the classification of alien species based on their residence time in Germany, including archaeophytes (alien species introduced before 1500 CE), and neophytes (introduced after 1500 CE) with the addition of invasive species (invasive neophytes; see (Richardson et al. 2000; Pyšek et al. 2004b) for definitions). We studied how functional diversity changes in the city of Halle (Saale), Germany. We selected relevant functional traits to examine the difference in functional diversity for native and alien plant species. Specifically, we studied: (1) functional diversity changes occurring during a 320-year period in the urban setting; (2) differences in the trajectories of functional diversity between native species and the three groups of alien species defined above, representing different stages of the invasion process; (3) functional diversity changes for specific functional traits related to urbanization processes (e.g. stress, competitiveness, and ecophysiology). Determining which plant groups (natives and alien) and functional traits benefit and which ones are disadvantaged by urbanization-related processes is important for understanding the mechanisms shaping the composition of urban floras, and for predicting trends in the future as the human population continues to move from rural to urban areas (DESA 2019).

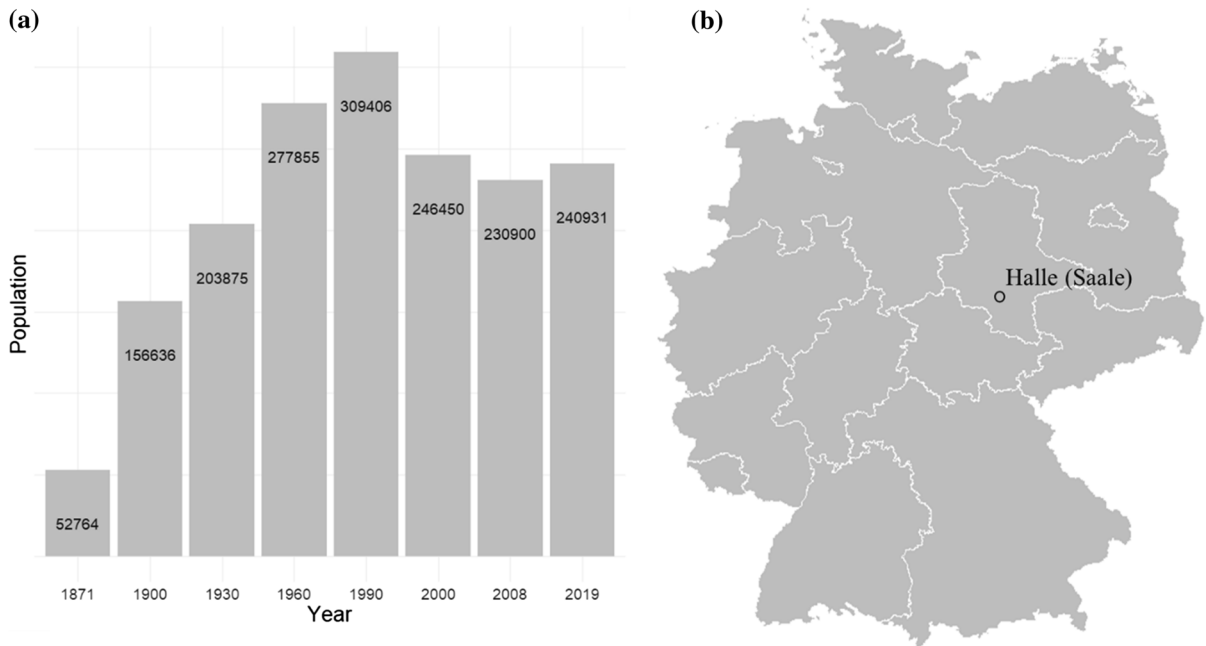
## Materials and methods

### Study area

The city of Halle (Saale) is located in central Germany (state of Saxony-Anhalt; Fig. 1b), east of the Harz Mountains (latitude of 51° 28' N; longitude 11° 58' E) with a mean elevation of 87 m a.s.l. (range 70–140 m; (Stolle and Klotz 2004). The city is located in the rain shadow of the Harz Mountains, with mean annual precipitation of only 497 mm and a mean annual temperature of 9.1 °C. Halle is traversed by the river Saale (for 27 km) which divides into several branches, forming small islets. Soils are highly heterogeneous, and the non-residential areas within the city predominantly consist of agricultural/horticultural land (~ 21%), forests (~ 10%), industrial and commercial areas (~ 9%), herbaceous flora/grasslands (~ 8%) and green urban areas (green and open spaces in the built-up area, 3%; Arnold et al. 2018). The original natural vegetation types in the area today covered by Halle (Saale) were mainly forests: alder, alder-ash, ash-elm, willow-poplar, oak-hornbeam, dry forests (Stolle and Klotz 2004). The current vascular flora comprises approximately 1400 species (Stolle and Klotz 2004). Areas for nature conservation mainly comprise alluvial forests and meadows as well as dry lawns on porphyritic rock (rhyolite). Halle (Saale) covers an area of about 135 km<sup>2</sup> and a population of 240 900 inhabitants (in 2019, Fig. 1a). There was a steady increase (since the beginning of recording in 1871) in population until the late 1980ies and a pronounced drop in the 1990ies due to the political changes in Germany. In recent years, population numbers stabilized.

### Historical data

First known records of Halle date from 806. The city started to extensively develop during the twelfth century. During the twentieth century, Halle expanded by incorporating several municipalities. In our analysis, we used historical floristic data on vascular plant species occurrences for the period 1687–2008. Historical records were related to the area within the present administrative borders of Halle with the help of site references given in historical publications. Historical data was composed of published species records performed by over 20 botanists since the late



**Fig. 1** Population development in Halle (Saale) for the period of 1871–2019, with changes in the number of inhabitants (y-axis) over time (x-axis) (a); location of Halle (Saale) in Germany (b)

**Table 1** Data sources of seven-time periods (1687–2008) for the study area (Halle (Saale), Germany) including published and unpublished inventories and herbariums (detailed information in Supplementary material S1b)

Timestep	Data source
1687–1689	Knauth (1687); improved edition 1989
1721–1783	Buxbaum (1721); Senckenberg (1731); Leysser (1761); Leysser (1783); Roth (1783)
1806–1856	Luyken (1806); Sprengel (1806); Wallroth (1815); Wallroth (1822); Garcke (1848); Garcke (1856)
1857–1901	Fitting et al. (1899); Fitting et al. (1901)
1902–1949	Fitting et al. (1903); Schulz & Wüst (1906); Schulz & Wüst (1907); Wangerin & Ule (1909); Schulze (1936; 1938); Knapp (1944a, 1944b); Knapp (1945)
1950–1999	Rauschert (1966a, 1966b, 1967, 1972, 1973, 1975, 1977a, 1977b, 1979, 1980, 1982); Grosse (1978, 1979, 1981, 1983, 1985, 1987); Grosse & John (1987); Grosse & John (1989); Grosse & John (1991); Klotz & Stolle (1998)
2000–2008	Stolle & Klotz (2005); unpublished data Stolle & Klotz (2005–2008)

seventeenth century, as well as manuscripts and herbarium records (Table 1). The accuracy of species occurrences was evaluated by Jens Stolle, a competent local botanist who made the following modifications. Species were excluded if (a) it is unlikely that the species occurred in the study area; (b) they occurred casually for a very short period; (c) they were merged into “superspecies”. Further, we included rare species with low dispersal capacity if they occur in Halle today but were not recorded by earlier botanists, assuming

that these species must have been overlooked in former times (for further details see Supplementary material S1a and Knapp et al. 2010).

We determined the total number of species and the number of unique species of every status group per time step (status groups categorized according to BiolFlor database, (Klotz et al. 2002), where time steps were distinguished based on publication dates of historical records (Fig. 2). We further distinguished invasive neophytes according to their negative impact,

following the KORINA (The Coordination Centre for Invasive Plants in protected areas of Saxony-Anhalt) blacklist of neophytes in Saxony-Anhalt (<http://www.korina.info>).

#### Trait data

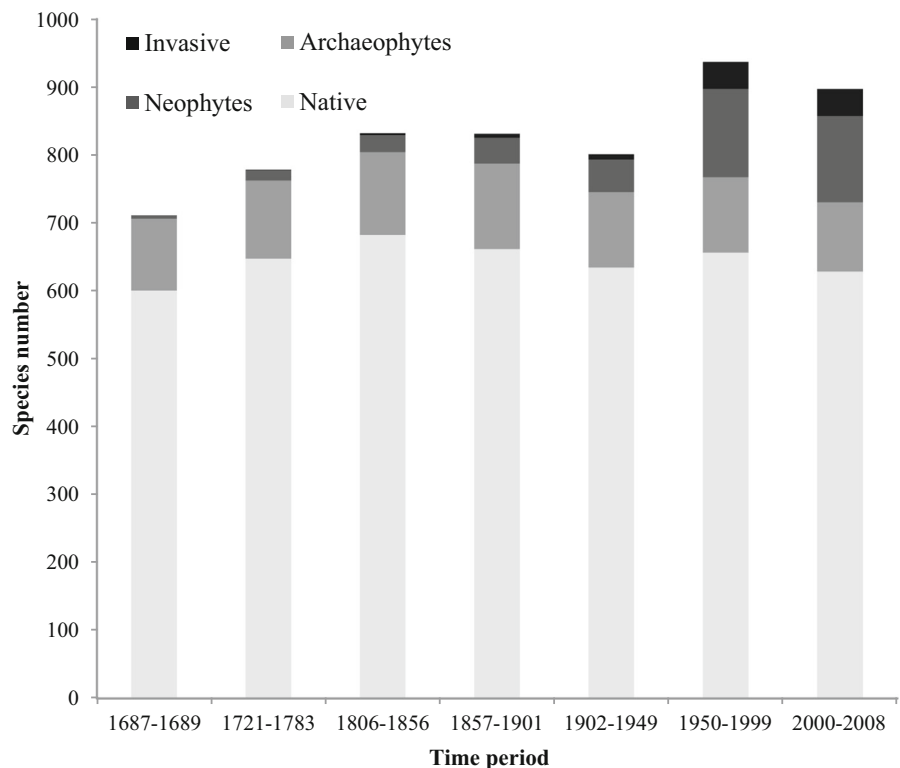
The traits were obtained from the BioFlor and LEDA databases (Table 2). Standards of trait measurement are explained in Kleyer et al. (2008) for LEDA and Klotz et al. (2002) for BioFlor. Regarding alien status, plant species were divided into native, archaeophytes, neophytes and invasive neophytes (Kühn et al. 2004; <http://www.ufz.de/biolflor>).

#### Data analysis

All data analyses were performed using R, version 3.6.1 (R Core Team 2017). Functional diversity was calculated for all selected functional traits (listed in Table 2) using the occurrences of every species. Occurrence matrices included the presence and absence of every species for each time step, while functional trait matrices included the categorical and

standardized (zero mean, unit standard deviation) numerical trait values for every species. Among the various indices for calculating FD, we chose RaoQ (Rao's quadratic entropy; Botta-Dukát 2005) as one of the most versatile and unbiased metrics for each trait per time step and status (Ricotta and Moretti 2011), using function *dbFD()* in the FD package (Laliberté and Shipley 2011). We selected multivariate RaoQ because it is suitable for multiple traits and it allows a mixture of categorical and continuous variables (Schleuter et al. 2010). RaoQ accounts for both functional richness and divergence (Mason and Bello 2013) as it includes species occurrences and the pairwise functional differences between species (Botta-Dukát 2005). RaoQ values increase with dissimilarity between traits of species and present abundance-weighted differences between species using their functional traits (Pavoine 2020). We checked for the independence of RaoQ among periods (temporal autocorrelation) using the *correlog()* function (ncf package, Bjornstad and Cai 2019). FD indices were not significantly autocorrelated and thus we did not need to account for temporal autocorrelation in the model.

**Fig. 2** Species number (y-axis) for seven-time periods (1687–2008) in Halle (Saale), Germany (x-axis) for the status groups native, archaeophytes, non-invasive neophytes, and invasive neophytes (different shades present four status groups)



**Table 2** List of functional traits, trait descriptions (trait states present sub-categories and their abbreviations of each trait, with value for numerical traits or class for categorical trait), and their sources

Trait	Trait states	Values	Source
Mean vegetative plant height	m	Metric	LEDA
Mean specific leaf area (SLA)	mm <sup>2</sup> /mg	Metric	LEDA
Mean seed mass	mg	Metric	LEDA
Flowering period	Beginning of flowering End of flowering Duration of flowering period	Months	BiolFlor
Storage organs	Presence Absence Multiple storage organs	Yes/No/Multiple	BiolFlor
Life form	Hydrophyte (A) Chamaephyte (C) Geophyte (G) Hemicryptophyte (H) Phanerophyte (P; including macrophanerophyte, nanophanerophyte, and hemiphanerophyte) Therophyte (T) Multiple life forms	A/C/G/H/P/T/Multiple	BiolFlor
Clonal growth organs	Presence Absence Multiple clonal growth organs	Yes/No/Multiple	LEDA
Pollination vector	Multiple pollination types Wind pollination Self-pollination (including two subgroups: selfing by a neighboring flower and selfing in an unopened flower) Insect pollination Pollination by water	Insect/Wind/Self/Water/ Multiple	BiolFlor
Ploidy	Diploid with haploid basic number Polyploid with haploid basic number Multiple	D/P/Multiple	BiolFlor
Leaf anatomy	Hydromorphic (A) Succulent (C) Helomorphic (E) Scleromorphic (S) Mesomorphic (M) Hygromorphic (Y)	A/C/E/S/M/Y	BiolFlor
Life span	Annual Pluriennial (including biennial) Multiple	A/P/Multiple	BiolFlor

Life form: *Hydrophyte* (survival buds submerged or floating on the water); *Chamaephyte* (a herbaceous or woody plant with buds on or few centimeters above the surface); *Geophyte* (species with storage organs protected underground); *Hemicryptophyte* (herbaceous species with buds lying on the ground protected by litter, leaves or stem); *Phanerophyte* (shrubs and trees, i.e. with buds located above the ground); *Therophyte* (short-lived annual herbs). Leaf anatomy: *Hydromorphic* (small number or lack of stomata, adapted to aquatic conditions); *Succulent* (drought-resistant species with water reservoirs in the leaves and restricted respiration); *Helomorphic* (many stomata and aeration tissue in the root to compensate for the lack of oxygen in the soil e.g. marshes, bogs); *Scleromorphic* (hard leaves with thick cuticle and epidermis); *Mesomorphic* (between scleromorphic and hygromorphic); *Hygromorphic* (thin cuticle and epidermis, species require relatively high humidity)

To test whether FD significantly changes over time for each status group and for which functional traits, we used linear regression with RaoQ as a response and status, time, all of the traits and interactions of the previous three groups as predictors. We also performed a test for normality for the transformed and untransformed dependent variable. Untransformed RaoQ values yielded the best model fits and were used in the analysis. For model selection, we used a multi-model inference approach (Burnham and Anderson 2002), employing the function *dredge* (package MuMIn, Barton 2015). For multiple posthoc comparisons between status groups, we used estimated marginal mean of linear trends (function *emtrends* from the package emmeans; Lenth et al. 2018), where all possible pairwise contrasts were tested. We performed post-hoc test (Tukey HSD pairwise comparisons for variable), comparing all 13 functional traits ('stats' package, R Core Team 2017). For graphical visualization, we used packages ggplot2 (Wickham et al. 2016) and maps (Becker et al. 2018).

## Results

### Functional diversity for different status groups

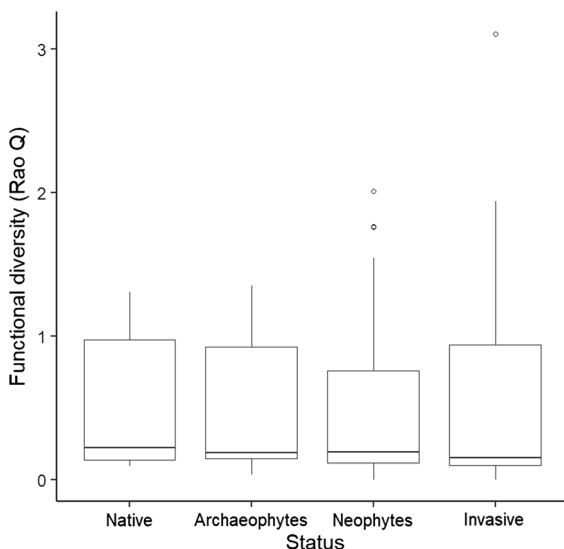
The recorded species numbers across time steps are: native 833, archaeophytes 141, neophytes 13, and invasive neophytes 40. Functional diversity (RaoQ) values range from  $4 \times 10^{-7}$  to 3.104. Average values of functional diversity (RaoQ) were highest for native species (Fig. 3), followed by archaeophytes, neophytes, with the lowest average functional diversity for invasive neophytes. The best model included  $\text{RaoQ} \sim \text{Status} + \text{Time} + \text{Trait} + \text{Status}:\text{Time} + \text{Status}:\text{Trait} + \text{Time}:\text{Trait}$ , and AICc weight of 0.963 which means that it is the most likely model of the ones tested; see S2 in Supplementary material). The second-best model had AICc weight 0.019 (with a delta AICc of 7.81). The best linear model had a high proportion of variation explained (78%), with FD of non-invasive and invasive neophytes differing significantly from native species (Table 3).

### Functional diversity changes over time for different status groups

The functional diversity (RaoQ) of native species did not significantly change over the seven time periods (Table 3b). Compared to native species, FD of neophytes and invasive neophytes increased significantly over time (Table 3d, Fig. 4). Pairwise comparisons showed that there was no significant difference between native species and archaeophytes or between alien groups (Table 4).

### Changes in FD for different traits for different status groups and over time

Except for the negative relationship of functional diversity (RaoQ) with height, there were no significant relationships for other functional traits using default settings, i.e. duration of flowering as reference trait (Table 3c). Performing a Tukey HSD post-hoc test, comparing all the traits, showed that almost two thirds of the 78 pairs of functional diversity values (RaoQ) of traits differ significantly from each other (see for details in Supplementary material S4). Compared to native species, archaeophytes did not show any significant difference in FD related to traits. Functional diversity (RaoQ) values for neophytes



**Fig. 3** Comparison of functional diversity (RaoQ) values (y-axis) for different status groups (native and alien plant species, x-axis). In the box plots, the black line presents median, vertical lines above and below the box indicate the 10th and 90th percentiles. Points above the lines indicate outliers outside the 10th and 90th percentiles

**Table 3** Multiple linear regression coefficients for predicting RaoQ as an index of functional diversity from explanatory variables (status, time and traits, a–c) and all two-way interactions (d–f) with significant differences in bold

Variable		S. E	t value	p
<i>Intercept</i>	0.00	0.97	– 0.43	0.67
<i>(a) Status</i>				
Archaeophytes	– 1.07	0.64	– 1.75	0.08
Neophytes	– <b>2.15</b>	<b>0.64</b>	– <b>3.53</b>	<b>0.00</b>
Invasives	– <b>2.82</b>	<b>1.10</b>	– <b>3.09</b>	<b>0.00</b>
<i>(b) Time</i>				
	0.16	0.00	1.44	0.15
<i>(c) Trait</i>				
Clonal growth organs	0.97	1.28	1.35	0.18
Duration of flowering	0.98	1.27	1.36	0.18
End of flowering	0.76	1.27	1.04	0.30
Height	– <b>1.79</b>	<b>1.27</b>	– <b>2.47</b>	<b>0.01</b>
Leaf anatomy	0.96	1.28	1.33	0.18
Life form	0.93	1.27	1.29	0.20
Life span	0.98	1.27	1.35	0.18
Ploidy	0.96	1.28	1.34	0.18
Pollination vector	0.96	1.27	1.33	0.19
Seed mass	0.24	1.27	0.34	0.74
SLA	– 0.40	1.27	– 0.55	0.58
Storage organs	0.99	1.27	1.36	0.17
<i>(d) Status × Time interaction</i>				
Archaeophytes:time	1.05	0.00	1.75	0.08
Neophytes: time	<b>1.99</b>	<b>0.00</b>	<b>3.33</b>	<b>0.00</b>
Invasives: time	<b>2.49</b>	<b>0.00</b>	<b>2.73</b>	<b>0.00</b>
<i>(e) Status × trait interaction</i>				
Archaeophytes: clonal growth organs	0.00	0.18	– 0.06	0.95
Invasives: clonal growth organs	0.09	0.21	1.78	0.08
Neophytes: clonal growth organs	0.05	0.18	0.87	0.38
Archaeophytes: duration of flowering	– 0.03	0.18	– 0.52	0.61
Invasives: duration of flowering	<b>0.13</b>	<b>0.21</b>	<b>2.47</b>	<b>0.01</b>
Neophytes: duration of flowering	0.11	0.18	1.91	0.06
Archaeophytes: end of flowering	0.00	0.18	0.06	0.95
Invasives: end of flowering	0.07	0.21	1.24	0.22
Neophytes: end of flowering	0.03	0.18	0.56	0.58
Archaeophytes: height	– 0.11	0.18	– 1.96	0.05
Invasives: height	– 0.06	0.21	– 1.20	0.23
Neophytes: height	– <b>0.13</b>	<b>0.18</b>	– <b>2.36</b>	<b>0.03</b>
Archaeophytes: leaf anatomy	0.00	0.18	– 0.05	0.96
Invasives: leaf anatomy	0.09	0.21	1.90	0.06
Neophytes: leaf anatomy	0.05	0.18	0.82	0.41
Archaeophytes: life form	0.01	0.18	0.20	0.85
Invasives: life form	<b>0.12</b>	<b>0.21</b>	<b>2.17</b>	<b>0.03</b>
Neophytes: life form	0.06	0.18	1.03	0.31
Archaeophytes: life span	0.02	0.18	0.37	0.71
Invasives: life span	<b>0.12</b>	<b>0.21</b>	<b>2.26</b>	<b>0.02</b>



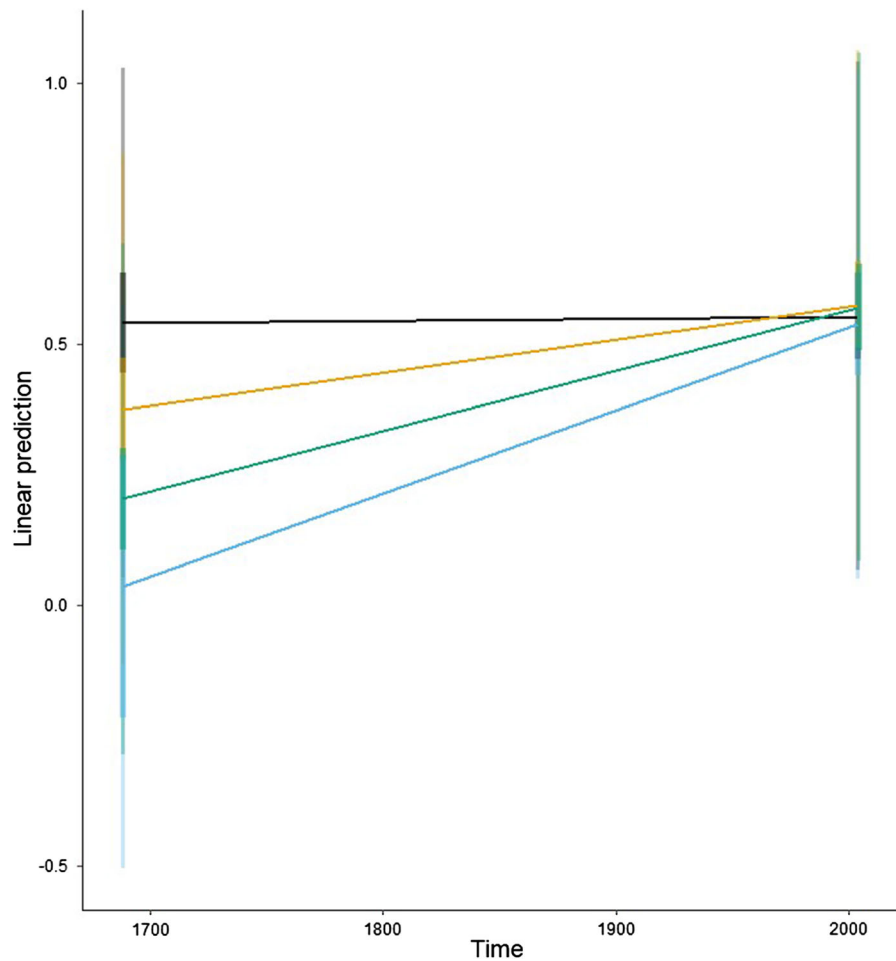
**Table 3** continued

Variable		S. E	t value	<i>p</i>
Neophytes: life span	0.08	0.18	1.36	0.17
Archaeophytes: ploidy	0.01	0.18	0.24	0.81
Invasives: ploidy	0.08	0.21	1.68	0.09
Neophytes: ploidy	0.06	0.18	0.99	0.32
archaeophytes: Pollination vector	0.01	0.18	0.25	0.80
invasives: Pollination vector	<b>0.11</b>	<b>0.21</b>	<b>2.10</b>	<b>0.03</b>
neophytes: Pollination vector	0.05	0.18	0.90	0.37
archaeophytes: seed mass	− 0.10	0.18	− 1.73	0.08
Invasives: seed mass	− <b>0.12</b>	<b>0.21</b>	− <b>2.32</b>	<b>0.02</b>
Neophytes: seed mass	− <b>0.23</b>	<b>0.18</b>	− <b>4.12</b>	<b>0.00</b>
Archaeophytes: SLA	0.03	0.18	0.62	0.54
Invasives: SLA	<b>0.14</b>	<b>0.21</b>	<b>2.59</b>	<b>0.01</b>
Neophytes: SLA	− 0.02	0.18	− 0.34	0.73
Archaeophytes: storage organs	− 0.01	0.18	− 0.25	0.80
Invasives: storage organs	<b>0.11</b>	<b>0.21</b>	<b>2.06</b>	<b>0.04</b>
Neophytes: storage organs	0.04	0.18	0.79	0.43
<i>(f) Time × trait interaction</i>				
Time: clonal growth organs	− 1.41	0.00	− 1.95	0.05
Time: duration of flowering	− 0.93	0.00	− 1.28	0.20
Time: end of flowering	− 0.74	0.00	− 1.03	0.31
Time: height	<b>1.79</b>	<b>0.00</b>	<b>2.46</b>	<b>0.01</b>
Time: leaf anatomy	− <b>1.46</b>	<b>0.00</b>	− <b>2.02</b>	<b>0.04</b>
Time: life form	− <b>1.45</b>	<b>0.00</b>	− <b>2.00</b>	<b>0.04</b>
Time: life span	− <b>1.48</b>	<b>0.00</b>	− <b>2.05</b>	<b>0.04</b>
Time: ploidy	− <b>1.43</b>	<b>0.00</b>	− <b>1.98</b>	<b>0.05</b>
Time: pollination vector	− <b>1.45</b>	<b>0.00</b>	− <b>2.00</b>	<b>0.04</b>
Time: seed mass	− 0.10	0.00	− 0.13	0.89
Time: SLA	0.33	0.00	0.46	0.64
Time: storage organs	− <b>1.43</b>	<b>0.00</b>	− <b>1.98</b>	<b>0.05</b>
Number of observations	<b>335</b>			
<i>R</i> <sup>2</sup>	<b>0.78</b>			
<i>Adj. R</i> <sup>2</sup>	<b>0.73</b>			
Residual Std. Error	<b>0.24 (df = 267)</b>			
F Statistic	<b>14.45*** (df = 67, 267)</b>			
<i>p</i> -value	<b>&lt; 2e<sup>−16</sup></b>			

β: standardized coefficient; S.E.: standard error of estimate; *p*: level of significance, \**p* < 0.05; \*\**p* < 0.01; \*\*\**p* < 0.001

(compared to native species) significantly decreased for height and seed mass (Table 3e). Invasive neophytes showed a significant increase in FD, compared to natives, for the duration of flowering, life form, life span, pollination vector, SLA, and storage organs, and a significant decrease for seed mass (Table 3e).

Height was the only functional trait significantly increasing over time compared to the reference trait (beginning of flowering), while leaf anatomy, life form, life span, ploidy, pollination vector, and storage organs significantly decreased over time (Table 3f, Fig. 5).



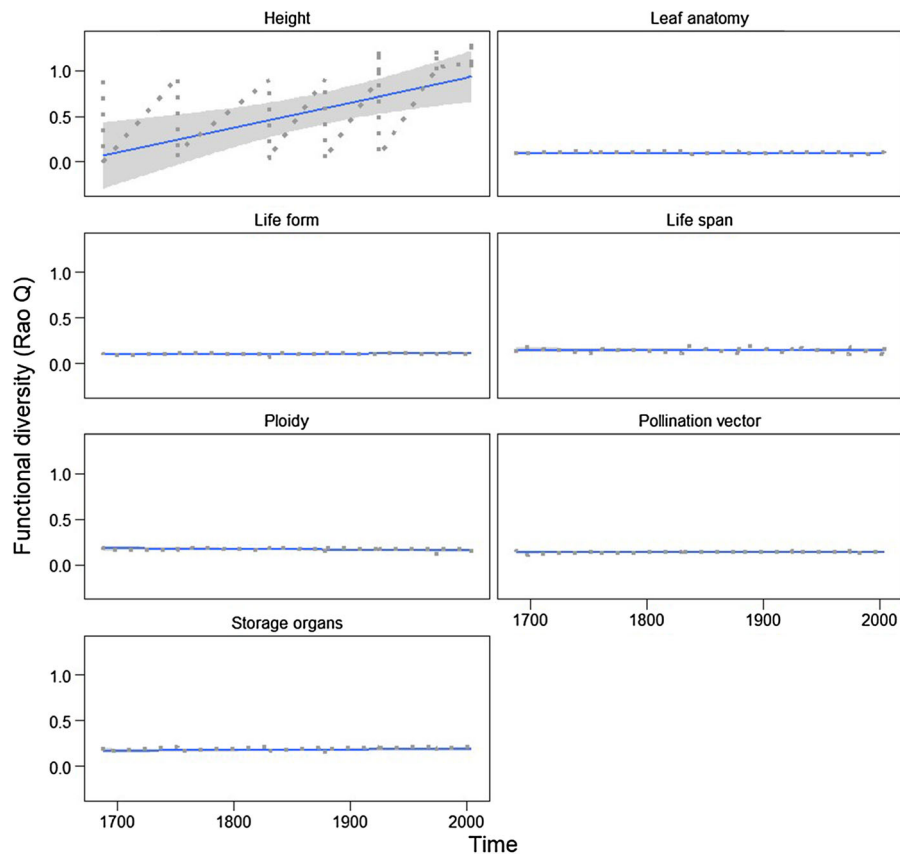
**Fig. 4** Pairwise interaction plot (based on the fitted model) for the estimated marginal means of linear trends. The figure shows linear predictions of the response variable (RaoQ) depending on the predictor variable (time) for native species (black) and alien

plant species (archaeophytes in yellow, neophytes in green and invasive neophytes in blue) at different stages of the invasion process with the 95% confidence interval

**Table 4** Pairwise comparison of estimated marginal means of linear trends between native species and alien plant species at different stages of introduction

Status	Estimate	S.E	t-ratio	p-value
Native × archaeophyte	− 0.0005	0.0003	− 1.751	0.29
<b>Native × neophyte</b>	− 0.0011	0.0003	− 3.326	<b>0.00</b>
<b>Native × invasive</b>	− 0.0015	0.0005	− 2.730	<b>0.03</b>
Archaeophyte × neophyte	− 0.0005	0.0003	− 1.575	0.39
Archaeophyte × invasive	− 0.0009	0.0005	− 1.693	0.39
Neophyte × invasive	0.0004	0.0005	0.760	0.87

Estimate presents the difference between the groups (corresponds to the difference in slope coefficients for the given comparison) with significant values in bold



**Fig. 5** Changes in predicted Functional diversity (RaoQ) over time (predictor variable) for all functional trait (predictor variables) which showed significant relationship. Colored lines

represent the linear regression line, and grey shading shows the 95% confidence interval of the fit

## Discussion

The species richness of the urban flora of Halle (Saale) increased over three centuries, however FD did not change over time. This suggests that on average species that colonized urban habitats as newcomers and those that went extinct were neither more nor less similar to the resident species. Compared with rural areas, urban areas in Europe are often hotspots of high plant diversity and particularly alien plant species (Haeupler 1974; Kühn et al. 2004; Kowarik 2011). We recorded an increase in native species (that are most likely locally introduced from surrounding regions) and an influx of neophytes, while there was a decrease in archaeophytes, probably as a result of arable land reduction on the account of urbanization (Jarošik et al. 2011). The disappearance of distinctive types of habitats resulted in the loss of some native species, while others might have been introduced or

immigrated into the city because of novel environmental conditions. Incoming native and alien species, as well as species remaining present across all time steps, possess traits that make them well adapted to these conditions (the strong filtering effect of urban environmental conditions; Williams et al. 2009; Aronson et al. 2016). The urbanization process begins with habitat transformation via loss and gain of novel habitats. Compared to rural areas, cities contain higher diversity of habitats, communities, and species (Sukopp 1998). For example, under an environmental gradient (e.g. temperature, precipitation, soil characteristics) species occupying a habitat will have a suite of functional traits that allow them to exist along the whole gradient represented in that habitat. In the case of environmental changes associated with urbanization, functional trait values might shift along the corresponding environmental gradient and thus some trait states can be lost or gained (Williams et al. 2015).

As the proportion of urban areas increased over time, semi-natural, nutrient-poor, and wet habitats were replaced by those habitats that were dry and nutrient-rich (typical for urban conditions; Pyšek et al. 2004b; Kowarik 2011). These novel habitats still foster a similar amount of variation of functional trait states as before, however, trait values or trait states change due to the presence of new species with different trait values. Accordingly, despite species turnover, overall FD does not change because new traits (which replaced previous traits) occupy a different part of the environmental gradient. For example, in Germany, novel ecosystems emerging from urbanization proved to be beneficial for alien plants (such as neophytes) but lead to homogenization in natives and archaeophytes (Kühn and Klotz 2006). Novel ecosystems are those ecosystems which are originally modified by humans and exhibit historically different abiotic and biotic properties (Hobbs et al. 2006). These novel environments influence interaction between species (or individuals) or directly affect organisms (Heger et al. 2019). Knapp et al. (2010) showed that trait composition in Halle shifted while here we show that variation stayed the same which might be due to loss and gain of environmental conditions at different ends of the cline. The results hence may imply that urbanization processes do not directly lead to a decrease in FD but rather a functional shift, by providing conditions for the same amount of functional variation as previous habitats. Further, habitats get more fragmented which leads to species extinction and introduction (emerging of new habitats and edge effect instigate introduction of new species; Fahrig 2003), as well as narrow functional trait range.

Environmental changes and human preferences are shaping urban flora (Williams et al. 2009), where functional traits either get confined or shift. Worldwide, 55% of people live in urban areas (DESA 2019). The level and rate of urbanization might influence species and functional diversity. Studies so far showed that moderate urbanization promotes species diversity (McKinney 2008), yet across the globe urban floras tend to share species, making urbanization a driver of biotic homogenization (McKinney 2006; Kühn and Klotz 2006). As the human population continues to rise, we can expect that the preference for certain species (Marco et al. 2008) will become more pronounced (e.g. preference for woody and ornamental species) and functionally more similar

communities will appear. For example, the size and colour of flowers and leaves as well as the selection of traits for ecological reasons such as tolerance to drought or “exoticness” of cultivated floras were shown to be important in urban landscapes (Kendal et al. 2012). Rapidly growing tree species introduced in the cities may alter ecosystem properties, e.g., carbon sequestration, erosion, water cycle, and soil organic matter (Castro-Díez et al. 2019). Further, in the urban areas of the United States, Dolan et al. (2011) found species turnover (loss of species preferring natural habitat, i.e., wetlands) to correlate with a decrease in native and an increase in alien species during the last 70 years. The increase in species diversity recorded in Halle can be attributed to an increase in the number of native species (immigrating from the regional species pool to Halle) and alien species (mainly neophytes) which were able to establish and spread after introduction (e.g. to abandoned urban areas; Bello et al. 2006).

#### Changes in functional diversity for different status groups

The increase in overall neophyte species richness and in that of invasive neophytes parallels the increase in their FD between 1687 and 2008, although FD for both groups remains lower compared to native species. Across all time steps, native species have both the highest species numbers and FDs while for invasive neophytes we recorded an increase in FD for multiple traits. Archaeophytes and non-invasive neophytes showed no difference or decrease in FD compared to the native group.

First, alien species responded with an increase in FD to urbanization, as they may be less limited by typical urban environmental conditions (fragmentation, urban heat island etc.) than native species, as many alien species are well adapted to these conditions and many of them possess high dispersal ability or are very fecund (Williams et al. 2009). The loss of natural habitats such as bogs, the gain of typical urban habitats (e.g. roadside vegetation, parks, modern residential areas, industrial estates) and competition between native and alien species over the last three centuries is likely to be the driver behind 22% species turnover in Halle (presence/absence of species between different time periods, previously reported by Knapp et al. (2010) as well as changes in FD.

Second, functional trait values for both continuous and categorical traits are getting similar over time which can be associated with environmental filtering (due to fragmentation or destruction of habitats, pollution, environmental stressors) and the limited number of potential niches. For example, land-use changes (e.g. transformation of natural or agricultural areas to urban) may promote the expansion of previously non-dominant native or alien species [e.g. woody species; (Díaz et al. 2007)].

Third, because of the marked increase in the number of established neophytes in Halle during the last centuries (and especially during the 1900s, where neophytes increased from 38 to 127 species, Fig. 2), there is a tendency for trait homogenization and communities are getting more functionally similar.

Alien species were shown to promote the homogenization of urban floras as themselves, being the drivers of change, or they adapt to and benefit from novel conditions and thus indicate habitat homogenization resulting from a process in which they act as passengers (MacDougall and Turkington 2005; HilleRisLambers et al. 2010). Species as drivers can become dominant (successful alien and native generalists) and alter environmental conditions. However, if the habitat conditions become more homogenized, species that are introduced and become naturalized have more similar functional traits, contrary to invasive species tend to be successful due to their dissimilarities (e.g. greater height compared to natives, archaeophytes and non-invasive neophytes; Divíšek et al. 2018). In Halle, both overall FD and trait FD remained constant over time for natives and species introduced more than five centuries ago (i.e. archaeophytes). Due to their long residence time, these alien species tend to stay functionally similar and thrive in homogenous habitats such as arable fields (Kühn and Klotz 2006).

#### Functional diversity of individual functional traits

As we observed a decrease in FD for many of the traits investigated, we can expect further filtering of species in the future and uniformity for traits such as life form, pollination vector, or life span. Our analysis demonstrated shifts in certain traits over time (counts of trait states per categorical trait and time step shown in Supplementary material S3), such as phenology expressed as the beginning of flowering. However,

focusing on the FD for specific groups, only invasive neophytes showed an increase in half of the studied traits, while archaeophytes and non-invasive neophytes did not differ from natives. As population growth and urbanization intensified in Halle from the seventeenth century onward, these developments affected species richness, composition, and functional traits. These effects are significant mainly because the changes due to urbanization are dramatic (great changes in the relatively short period) and usually encompass large areas (McKinney 2006). For most of the traits a meta-analysis by Williams et al. (2015) did not find consistent responses to disturbances in urban areas, with the exceptions of increasing values of plant height and seed mass. However, we found that height was the only trait showing an increase in FD over time and this might be because urban areas can promote a wide range of different plant heights. Over the last 5000 years, forest cover decreased, and forests were particularly reduced in the eighteenth century (at the beginning of our study period). Prussians started reforestation of the area in the late nineteenth century (Albrecht et al. 1993). This indicates that during the first time steps only species with specific heights were dominant (either tall or shorter species) and in proceeding periods (following replanting of the forest) we can observe an increase in height heterogeneity. Additionally, a wide range of heights in the urban area can be attributed to habitat transformations where smaller and short-lived ruderal species (growing along roads, railway or on brownfields) can increase in abundance, and to competition as taller species can be successful in competing with shorter species and human preference and cultivation. Taller species (trees and shrubs) are introduced to parks and gardens, and some of these species escape and establish—this process takes decades to centuries, depending on species (Kowarik 1995b). Since cities provide different types of habitats many species can grow spontaneously and colonize these areas.

Further, we found a decrease in FD for life form and life span over time, which might be related to habitat loss and environmental changes as a result of urbanization. Extinction of many species which leads to homogenization of functional traits is associated with the disappearance of specific habitats (Pykälä 2019) and conditions (e.g. bogs, wet meadows; Knapp et al. 2010) which lead to loss of respective traits. Furthermore, many phanerophytes (Table 2) are successful in

urban areas since they are favoured for their ornamental value and often cultivated in parks and gardens. Certain life forms i.e. therophytes (abundant in the cities due to high soil fertility and habitats with high disturbance, Table 2) often compete with other groups.

Functional diversity of SLA (specific leaf area) did not change over time, possibly because extreme values (both low and high) of SLA may prove to be beneficial in cities (Thompson and McCarthy 2008). Climatic limitations are particularly favourable for plant species characterized by idiosyncratic trait states (or extreme values) rather than facilitating heterogeneity for most functional traits. For example, higher temperature and aridity (characteristic for urban areas and aridity particularly prominent in Halle) promotes a decrease of SLA, while high nutrient availability in the soil leads to an increase in SLA values. Changes in precipitation primarily affect species with different leaf types. Halle's dry climate promotes plant species adapted to drought, i.e. species with scleromorphic or mesomorphic leaf types are prevailing over other types. Further, urban areas with lower air moisture are advantageous for wind-pollinated species, considering that under these conditions chances of pollen reaching flower stigma are higher (Knapp 2010). Genetic traits (i.e. ploidy level) may have the potential in explaining species establishment and colonization of new habitats. Polyploidy (high ploidy levels) is an important trait of alien and invasive species, affecting the probability of invasion success (Te Beest et al. 2012) and they might be more flexible and able to grow in different habitats (genetic variability leads to adaptation under new environmental conditions; Winter et al. 2008). Winter et al. (2009) showed that homogenization resulted from losing native species with unique traits and gaining alien and native generalist species. Functional homogenization can be further promoted in disturbed urban areas, as generalist species increase in numbers and potentially replace specialist species.

Our results showed that over the past 320 years, functional diversity increased for invasive and non-invasive neophytes, while overall, it remained constant. Parallel to the development of an urban area, functional diversity of native and alien species homogenized for the majority of traits investigated. As worldwide, many cities are growing, outcomes of studying historical data can be widely applicable. Further, integrating historical data and environmental

parameters would provide a rigorous representation of past floras and support the prediction of future biodiversity changes due to urbanization.

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**Data availability statement** The traits were obtained from the BioFlor (<http://www.ufz.de/biolflor>) and LEDA (<https://uol.de/en/landeco/research/leda/data-files>) databases. List of invasive species for Saxony-Anhalt was obtained from KORINA project (<http://www.korina.info>). The list of species used here is available as supporting information to Knapp et al. (2017), J. Appl. Ecol. 54 (4), 1152–1160 at <https://doi.org/10.1111/1365-2664.12826>.

#### Declarations

**Conflict of interest** All the authors declare that there is no conflict of interest.

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