Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization

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Summary

1. Urbanization is increasing faster than ever, contributing to a global extinction crisis. Recently, scientists have debated whether species richness on local and regional scales is mostly declining, but long-term changes in phylogenetic richness and divergence were largely disregarded. Space-for-time approaches revealed that plant phylogenetic divergence is lower in urban than in non-urban areas. However, such approaches cannot fully disentangle the relative importance of the biotic processes that drive temporal changes in diversity.
2. Using a unique European urban flora covering 320 years in seven time steps, combined with a comprehensive plant phylogeny, we examined (i) how species richness changed with urbanization over time; (ii) whether trends in phylogenetic richness and divergence parallel trends in species richness; and (iii) whether species extirpation or immigration is driving these changes.
3. We found that over time urban species richness increased, but phylogenetic richness and divergence decreased. Extirpations of phylogenetically distinct native species and immigrations of phylogenetically common native and non-native species caused a non-random loss of phylogenetic diversity. Our analyses suggest that if future extirpations and immigrations continue to follow the patterns observed over history, this loss will continue.
4. *Synthesis and applications.* Measures to protect phylogenetic diversity should combine the protection of threatened habitats and their species with the maintenance of habitats that mitigate heat and safeguard evolutionary history. Urban planners should consider a phylogenetically diverse set of species when designing green spaces.

Key-words: biological invasions, evolutionary history, extirpation, immigration, long-term ecological research, phyloecology, phylogenetic diversity, red-list species, species richness, urbanization

Introduction

Human actions have deeply altered planet earth leading to a global extinction crisis (Barnosky *et al.* 2011). Although there is strong evidence that globally more and more species are threatened with extinction, we are not certain about numbers of local and regional extinctions and thus also not about change in biodiversity at those scales (Thomas 2013). Recent studies, for example, did not find net losses in local species richness across taxa and habitats at global scale (Vellend *et al.* 2013; Dornelas *et al.* 2014). They did find, however, marked changes in species composition over time and highlighted the need to understand the consequences of such changes. Many studies on temporal changes in biodiversity, however, consider only one measure of biodiversity: species richness, although it is widely accepted that we need to understand the responses of functional or phylogenetic diversity to global change as well (Cadotte, Carscadden & Mirotchnick 2011). From a conservation perspective, phylogenetic diversity is important, since there is evidence that greater phylogenetic diversity leads to a higher ecosystem stability (e.g. Flynn *et al.* 2011; Pu *et al.* 2014; but see Venail *et al.* 2015) and to higher diversity across trophic levels (Dinnage *et al.* 2012). Moreover, as unique biodiversity components per se depict millions of years of

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evolutionary history, the conservation of phylogenetic diversity in the light of the biodiversity crisis is an urgent issue to be tackled.

Generally, our understanding of temporal changes in biodiversity is hampered by the fact that most studies look at relatively short time spans of 50–200 years only (McGill *et al.* 2015); i.e. species extinctions due to major land-use changes might either had happened earlier or might not have happened, yet ('extinction debt'; Hahs *et al.* 2009). Moreover, long-term monitoring sites are rarely revisited once they have been converted into different land-use types (Cardinale 2014), and thus, we might underestimate species losses because we do not monitor them properly.

One main type of land-use conversion is urbanization, which is increasing faster than ever (Secretariat of the Convention on Biological Diversity 2012). Urbanization can promote the extinction of native species, the immigration of common, disturbance-tolerant native species (Beauvais, Pellerin & Lavoie 2016) and the immigration of non-native species, changing not only the taxonomic but also the functional and phylogenetic composition of species assemblages (Knapp *et al.* 2008; Williams, Hahs & Vesk 2015). However, most studies that assessed the effects of urbanization on plant phylogenetic diversity relied on space-for-time approaches (e.g. Knapp *et al.* 2008; Ricotta *et al.* 2009; Čeplová *et al.* 2015) – basically due to a lack of temporal data along land conversion. Space-for-time approaches, however, neglect that land-use change is a process that has affected biodiversity since millennia. Thus, while space-for-time approaches revealed increasing relatedness (i.e., decreasing phylogenetic divergence) of vascular plant species in urban as compared with non-urban areas (e.g. Knapp *et al.* 2008), these studies could not fully disentangle the relative importance of the main biotic processes that drive the loss of phylogenetic diversity over time, such as extirpation and immigration.

Here, we take advantage of a unique floristic data set (Table S1, Supporting Information) from central Germany that spans 320 years of compositional changes of plant assemblages in an area that was transformed from an agricultural landscape including a small town into an urban landscape. We examine
1. How the species richness of vascular plants changed with increasing urbanization over this 320-year period,
2. Whether trends in phylogenetic richness and divergence (as measures of phylogenetic diversity) parallel trends in species richness and
3. Whether species (local) extinction (extirpation) vs. immigration drive phylogenetic changes to different degrees.

Herewith, we aim to explore whether species extirpation or immigration is random with respect to phylogeny (not selecting for specific clades within the tree of life) or whether these changes show phylogenetic signal (either selecting for close relatives or for species that are less related than expected at random). In addition, we explore how patterns of phylogenetic diversity would change if (i) today's red-list species were extirpated from the study area and (ii) immigration of non-native species continued.

Materials and methods

STUDY AREA

The study area comprises today's administrative district of the city of Halle (Saale), central Germany (135 km² in size; with its centre at 11°58′19″E, 51°28′59″N; Fig. S1). Climate is subcontinental with mean annual temperatures of 9 °C, mean monthly temperatures between 0 and 19 °C, and 480 mm of mean annual precipitation peaking in summer (reference period: 1961–1990; Müller-Westermeier, Kreis & Dittmann 1999, 2001). Elevation ranges from 71 to 136 m a.s.l. (www.halle.de).

The city's extent increased within the study period (from 1687 to 2008). Still, throughout the study, we refer to today's administrative district and not to historical administrative districts. Consequently, the study area today includes the city of Halle, but the city and its immediate rural surroundings in former times. Old maps show that before the 20th century, the study area was dominated by agriculture with few patches of forest. Identifying those species that in former times occurred within today's administrative district was possible with the help of site references given in the floristic inventories used in this study (cf. Table S2).

Within the study period, Halle's population increased (due to both the incorporation of villages and population growth) from 21 000 inhabitants in 1820 to 231 800 inhabitants in 2008 (numbers earlier than 1820 are not available; Stolle & Klotz 2004).

PLANT SPECIES DATA OF THE PAST

Most urban floras do not exceed a historical range of 40–200 years, as shown in a global literature survey (Hahs *et al.* 2009). In contrast, our data set covers a period of 320 years. More than 20 botanists published their species records from the Halle area between the end of the 17th (1687) and the onset of the 21st century (2008; Table S2), with a number of published historical and recent floras as well as smaller manuscripts and herbarium entries covering large parts of the 18th, 19th, 20th and 21st centuries. Inventories were not restricted to species of pharmaceutical interest, as it had been common until the 16th century, but cover the whole range of species.

Each historical flora was assessed for reliability (cf. Knapp *et al.* 2010) by a highly experienced botanist who is familiar to the regional flora (cf. Acknowledgements): (i) Species that are unlikely to ever have occurred in the study area were excluded as ill-determined. (ii) If a rare native species with low dispersal capacity occurs in the study area today but was not mentioned in historical records, we assumed that it also occurred in former times (it might have been overlooked). (iii) Species that could not be assigned to modern nomenclature were excluded (nomenclature from the 17th and early 18th centuries is pre-Linnean, as Carl von Linné published 'Species Plantarum' in 1753; Linnaei 1753). (iv) If species that we distinguish today were not distinguished earlier, we used the historical standard – species distinguished today can be merged into the former standard but not vice versa.

CLASSIFYING PLANT SPECIES DATA OF THE PAST: NATIVE STATUS, EXTIRPATION AND IMMIGRATION

We focussed on spontaneous species, i.e. species that do not rely on human assistance (in contrast to species that are exclusively cultivated). We divided plant records into seven groups, according to the time of recording (Table S2): (i) 1687–1689, (ii) 1721–1783, (iii) 1806–1856, (iv) 1857–1901, (v) 1902–1949, (vi) 1950–1999 and (vii) 2000–2008. Further, we distinguished species native to Germany from species not native to Germany (Kühn, Durka & Klotz 2004; http://www2.ufz.de/biolflor). Non-native species comprise all neophytes except for casual species (non-native species that occurred in one time step but vanished again in a subsequent time step). Neophytes are plant species that immigrated or were introduced after the discovery of the Americas by Columbus, with the year 1500 as threshold (Pyšek *et al.* 2004). This threshold is used in invasion ecology because prior to 1500, species not native to Central Europe mainly came from the Mediterranean or Middle East, while after 1500 species were introduced from around the world. Concordantly, we lumped species native to Germany together with archaeophytes (pre-1500 aliens) as for some archaeophytes it is hard to distinguish whether they are really archaeophytes or native (Pyšek *et al.* 2004).

We further distinguished between native species that became extirpated after the end of the 17th century (i.e., after the first time step 1687–1689), native species that immigrated after the end of the 17th century (called 'native immigrants' from now on), and non-native species that immigrated after the end of the 17th century ('non-native immigrants').

In summary, we analysed historical records for the (i) total flora, native flora and non-native flora across time steps and (ii) extirpated species, native immigrants and non-native immigrants.

PLANT SPECIES DATA OF THE FUTURE

To estimate how potential future extirpation and immigration will affect phylogenetic diversity, we additionally selected (i) today's threatened species, i.e. native species that occurred in our study area in the early 21st century (last time step, 2000–2008) and that are listed as critically endangered, endangered or vulnerable in Germany (Ludwig & Schnittler 1996); (ii) potential future non-native immigrants, i.e. neophytes that today occur in at least 20% of Germany (derived from Florkart – the data base of the floristic mapping of Germany; http://www.floraweb.de) but that were not present in Halle in the last time step, yet. Out of all non-native species that today occur in Germany, 405 do not occur in Halle, yet. Still, most of them are rare and seem unlikely to spread much further in near future. Thus, we used a minimum distribution of 20% of Germany's area to only include frequent non-native species.

SPECIES RICHNESS

We calculated species richness per time step for the total flora, the native flora and the non-native flora. After testing for normal distribution using Kolmogorov–Smirnov test, we tested for significant trends in species richness between 1687 and 2008 using simple linear models (with species richness as response and time as predictor). We compared these models to intercept-only models by applying Akaike's information criterion (AIC). The model with the smallest AIC is preferable (Akaike 1974).

PHYLOGENETIC DATA AND MEASURES OF PHYLOGENETIC DIVERSITY

Phylogenetic data was taken from Daphne (Durka & Michalski 2012, 2016), a dated phylogeny covering the vascular flora of the British Isles, Germany, The Netherlands and Switzerland, totalling 4685 species. By using R (R Core Team 2014), Daphne was pruned to (i) the total flora, (ii) native species and (iii) non-native species per time step, (iv) extirpated species, (v) native immigrants, (vi) non-native immigrants, (vii) today's threatened species and (viii) potential future non-native immigrants (Fig. S2, provides a phylogenetic tree of the flora).

Various indices exist for quantifying phylogenetic diversity, which differ in their meaning and way of calculation (Tucker *et al.* 2016). Measures of phylogenetic richness 'sum up the quantity of phylogenetic differences present in an assemblage' (Tucker *et al.* 2016, p. 4); measures of phylogenetic divergence 'average the distribution of units extracted from a phylogenetic tree' (Tucker *et al.* 2016, p. 4). We chose a common measure of phylogenetic richness, i.e. PD (Faith 1992), which measures the sum of all branch lengths present in a phylogenetic tree and is directly comparable to species richness. Moreover, we used one measure of phylogenetic divergence, i.e., average phylogenetic distinctness (AvPD), which had been derived from taxonomic distinctness (Clarke & Warwick 2001) and measures the average pairwise distance over all species in a phylogenetic tree in order to asses changes in the phylogenetic uniqueness of the flora.

Temporal changes of PD and AvPD indicate how mean phylogenetic richness and divergence change over time. Still, they do not indicate whether observed trends are random across the phylogeny, clustered (species more closely related than expected at random) or overdispersed (species less closely related than expected at random). To test whether species that became extirpated or that immigrated in the past as well as today's threatened species and potential future non-native immigrants are phylogenetically clustered, overdispersed or random, we applied D (Fritz & Purvis 2010). D measures phylogenetic signal in a binary trait (e.g. extirpated vs. not extirpated), comparing observed values to values expected under Brownian evolution or random evolution, respectively. Brownian evolution indicates that the binary trait is phylogenetically conserved (i.e., shared among close relatives). Random evolution indicates that the binary trait distributes among species without any phylogenetic signal. Values of D close to 0 indicate Brownian evolution; values close to 1 indicate random evolution. Values between 0 and 1 that significantly differ from 1 indicate that there is a phylogenetic signal, with its strength depending on the value of D (e.g., $D = 0.5$ can be termed 'moderately clustered'; $D = 0.8$ 'weakly clustered'; Fritz & Purvis 2010).

TRENDS IN THE PHYLOGENETIC RICHNESS AND DIVERGENCE OF THE PAST

We calculated PD and AvPD per time step for the total flora, the native flora and the non-native flora using the R-packages 'picante' (Kembel *et al.* 2010) and 'vegan' (Oksanen *et al.* 2013). To test for significant trends of PD and AvPD over time, we applied simple linear models as described for species richness (including comparisons to intercept-only models with AIC).

Second, we calculated PD and AvPD for all native species that became extirpated after the end of the 17th century and for both native and non-native immigrants. As this only yields one value

per group, we applied random sampling: We calculated PD and AvPD for 999 random draws out of all late 17th-century species, with each random sample having the same number of species as there were extirpated species or native or non-native immigrants, respectively. Observed and random values were compared using Wilcoxon rank-sum test. This showed whether extirpated species and immigrants are more or less closely related than the late 17th-century species.

To test whether trends in PD and AvPD hold after excluding the first two time steps (17th and 18th centuries; being the oldest and, therefore, those with highest uncertainties), we redid all calculations, using the third time step (1806–1856) as basis, not considering the 17th and 18th centuries but only considering the last 200 years ('quality check').

POTENTIAL TRENDS IN THE PHYLOGENETIC RICHNESS AND DIVERGENCE OF THE FUTURE

To test the effect of (i) losing today's threatened native species and (ii) gaining more non-native species on PD and AvPD, we combined species as follows: The 'future flora' consists of the total flora of the last time step (2000–2008) plus potential future non-native immigrants ($n = 24$) but without today's threatened species ($n = 74$), as these are hypothesized to become extirpated in the future. Accordingly, the 'future native flora' consists of all native species present in 2000–2008 but excluding the threatened ones, while the 'future non-native flora' consists of all non-native species present in 2000–2008 plus potential future non-native immigrants. We calculated PD and AvPD for the total, the native and the non-native future flora. Afterwards, we combined this 'future time step' with the seven historical time steps and tested for significant trends in PD and AvPD over time by using simple linear models (again with time as sole predictor). Moreover, we compared PD and AvPD of all threatened species and of all potential future non-native immigrants with random samples from the total flora of the last time step by using Wilcoxon rank-sum test (random samples contain as many species as there are threatened species or potential future non-native immigrants, respectively).

PHYLOGENETIC SIGNAL OF PAST AND FUTURE EXTIRPATION AND IMMIGRATION

Using function 'phylo.d' in R-package 'caper' (Orme *et al.* 2013), we measured phylogenetic signal (D) in the following binary groups: (i) native flora of the late 17th or early 19th century vs. native species that became extirpated after the late 17th or early 19th century; (ii) native flora of the late 17th or early 19th century vs. native immigrants from after the late 17th or early 19th century; (iii) total flora of the late 17th or early 19th century vs. non-native immigrants from after the late 17th or early 19th century; (iv) native species not threatened vs. native species threatened in the early 21st century; (v) total flora of the early 21st century vs. potential future non-native immigrants.

Results

PLANT SPECIES DATA OF THE PAST

We excluded five species as ill-determined and three species as exclusively cultivated. In 344 cases, we assumed that a species had been overlooked. This was especially the case for the first time step (1687–1689) with 268 species that had been recorded in the subsequent time steps but not the first time step itself. The same applied to 56 species in the second (1721–1783), 18 species in the third (1806–1856) and one species in each the fourth (1887–1901) and fifth time step (1902–1949). This indicates that floristic surveys have become more comprehensive since the 17th century.

In 28 cases, native species disappeared in one time step, but reappeared in a subsequent time step. These species were not classified as 'extirpated' but counted as always present, and 12 non-native immigrants were excluded as casuals.

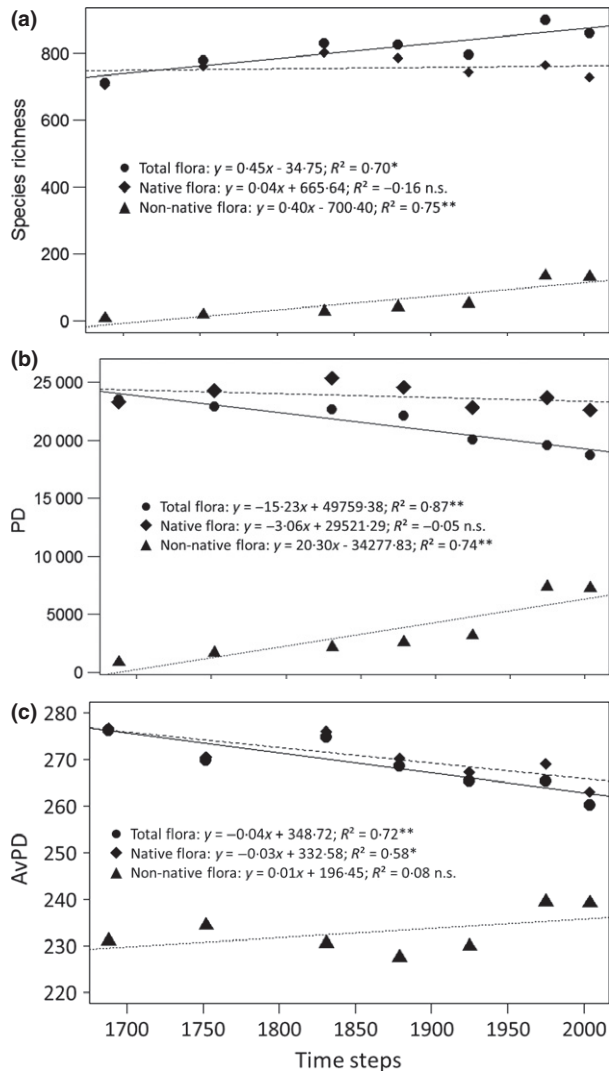### TRENDS IN THE PLANT SPECIES RICHNESS OF THE PAST

We observed a significant increase in total plant species richness between 1687 and 2008 (Fig. 1a, Table S3). The increase from 711 species to 860 species ($R^2 = 0.70$; $P < 0.05$) was mainly driven by the 22-fold increase in non-native species (from 6 to 130 species; $R^2 = 0.75$; $P < 0.01$). The number of native species increased from 705 to 729 species, but statistically, this was not significant ($R^2 = -0.16$; $P > 0.1$; intercept-only model preferable; Table S4).

Total species richness still increased (from 830 to 860 species; $R^2 = 0.08$; $P > 0.1$) after omitting the first two time steps ('quality check'; see Methods). Statistically, this increase was not significant (intercept-only model preferable). 'Quality-checked' native species richness slightly decreased, but this trend was statistically not significant ($R^2 = 0.67$; $P > 0.05$; intercept-only model preferable). Numbers of non-native species kept increasing ($R^2 = 0.82$; $P < 0.05$). As the overall trends in species richness stayed the same, no matter whether including or excluding the first two time steps, we assume that the quality of the two oldest data sets is sufficient (moreover, results for PD and AvPD did not change when applying quality check).

In total, 157 native species became extirpated, while 181 native species and 125 non-native species immigrated to the study area (Table S5, 'extirpated' always refers to the loss of species from the study area and not to the global extinction of a species).

TRENDS IN THE PHYLOGENETIC RICHNESS AND DIVERGENCE OF THE PAST

In contrast to increasing species richness, the phylogenetic richness of the total flora decreased from PD = 23 483 myr in the first time step to PD = 18 739 myr in the last time step ($R^2 = 0.87$; $P < 0.01$; Fig. 1b, Table S6). For the native flora, PD decreased as well (from PD = 23 297 myr to PD = 22 615 myr), but statistically, this trend was insignificant ($R^2 = -0.05$; $P > 0.1$;

Fig. 1. Trends in the (a) species richness, (b) phylogenetic richness (PD in millions of years) and (c) phylogenetic divergence (AvPD in millions of years) of the total flora (dots, solid line), the native flora (diamonds, dashed line) and the non-native flora (triangles, dotted line) in the city of Halle (Saale), Germany, between 1687 and 2008. For each trend line, model parameters are shown (R^2 is adjusted for number of predictors P-values: $P > 0.05$ n.s.; $0.05 > P > 0.01$*; $0.01 > P > 0.001$**).

intercept-only model preferable; Table S4). The immigration of non-native species significantly increased PD (from 853 to 7258 myr; $R^2 = 0.74$; $P < 0.01$) but not AvPD ($R^2 = 0.08$; $P > 0.1$), indicating a gain of species closely related to those already occurring in the study area (Fig. 1c, Table S7). AvPD of the total flora decreased by 16.18 myr ($R^2 = 0.72$; $P < 0.01$), mainly driven by a compositional change in native species, which led to a loss of 13.61 myr of average relatedness ($R^2 = 0.58$; $P < 0.05$).

PD of extirpated species and of non-native immigrants did not differ from random values. PD of immigrated native species was marginally smaller (PD = 8970 myr) than random values (PD$_{random\ 17th\ century,\ mean}$ = 9968 myr).

AvPD of extirpated native species was higher (AvPD = 311.55 myr) than for the late 17th-century species (AvPD = 276.39 myr) and also higher than for native immigrants (AvPD = 252.99 myr) and for non-native immigrants (AvPD = 239.34 myr). Moreover, extirpated native species were more distinct than random species assemblages (AvPD$_{random\ 17th\ century,\ mean}$ = 275.19 myr), while both non-native and native immigrants were less distinct than random species assemblages (AvPD$_{random\ 17th\ century,\ mean}$ = 272.04 myr for non-native immigrants and = 276.4 myr for native immigrants). This indicates the loss of evolutionary distinct native species and the gain of evolutionary common native and non-native species – a trend that is likely to continue (see below).

POTENTIAL TRENDS IN THE PHYLOGENETIC RICHNESS AND DIVERGENCE OF THE FUTURE

Of all plant species present in the study area in the early 21st century, 74 have been listed as critically endangered, endangered or vulnerable in Germany (Ludwig & Schnittler 1996). Moreover, we identified 24 non-native species as occurring in more than 20% of Germany but not in Halle, yet. If the 74 threatened species became extirpated and the 24 non-native species immigrated to Halle in the future, PD and AvPD would further decrease for both the total flora (PD: $R^2 = 0.12$; $P > 0.1$; AvPD: $R^2 = 0.80$; $P < 0.01$) and the native flora (PD: $R^2 = 0.25$; $P > 0.1$; AvPD: $R^2 = 0.70$; $P < 0.01$) although these trends were statistically not significant for PD (Fig. 2). For the non-native flora, PD ($R^2 = 0.82$; $P < 0.01$) and AvPD ($R^2 = 0.18$; $P > 0.1$) would keep increasing, but this trend was only significant for PD (Fig. 2). With AvPD = 275.55 myr, threatened species were more distinct than the early 21st-century flora (Table S7). PD was not different for the threatened vs. early 21st-century flora. With PD = 1628.65 and AvPD = 224.07, both the observed phylogenetic richness and divergence of potential future non-native immigrants were smaller than the richness and divergence of species present in the early 21st century.

PHYLOGENETIC SIGNAL OF PAST AND FUTURE EXTIRPATION AND IMMIGRATION

In comparison to the late 17th-century native flora, extirpated species were weakly but significantly clustered ($D = 0.85$; Table 1), i.e., their distribution within the tree of life was non-random. Native immigrants, non-native immigrants, potential future non-native immigrants and today's threatened native species were clustered more strongly than extirpated species (Table 1). Consequently, urbanization led to both the loss of native species from certain evolutionary clades and to the establishment of non-native species from certain clades.
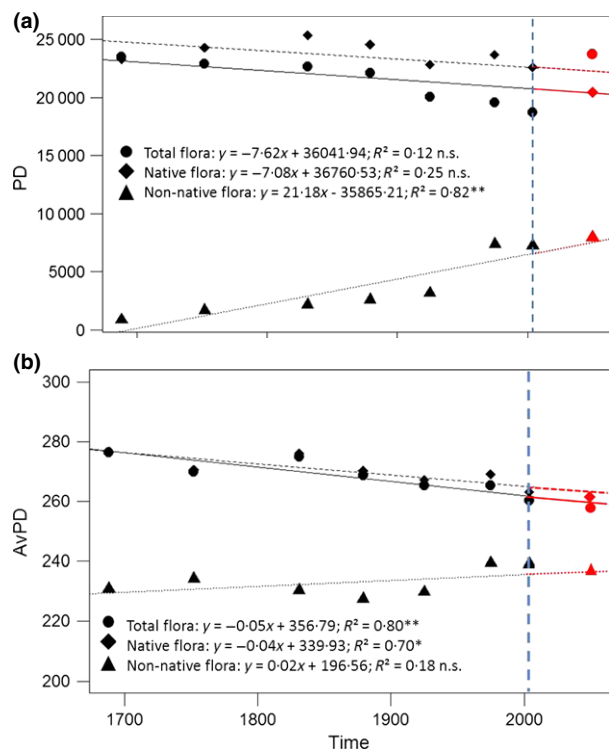
Fig. 2. Black lines and symbols resemble data in Fig. 1, i.e., trends in the (a) phylogenetic richness (PD; in millions of years) and (b) divergence (AvPD in millions of years) of the total flora (dots, solid line), the native flora (diamonds, dashed line) and the non-native flora (triangles, dotted line) in the city of Halle (Saale), Germany, between 1687 and 2008. Red lines and symbols (set at time = 2050) illustrate the potential future development of PD/AvPD in case (i) all threatened native species present in Halle today (2000–2008) became extirpated; (ii) non-native species that today occur in more than 20% of Germany but not in Halle yet immigrated. The vertical dashed blue line marks the endpoint of our historical data set and the start of our projection into the future. For each trend line, model parameters are shown (R^2 is adjusted for number of predictors; P-values: $P > 0.05$ n.s.; $0.05 > P > 0.01^*$; $0.01 > P > 0.001^{**}$). [Colour figure can be viewed at wileyonlinelibrary.com]

Table 1. Phylogenetic signal in extirpation and immigration for the past and future flora of the city of Halle ('Binary trait') expressed as *D* (Fritz & Purvis 2010). P ($D > 0$) and P ($D < 1$) indicate whether phylogenetic signal is significantly different from Brownian motion (phylogenetically conserved) or random (not conserved), respectively

Binary trait	Number of species	*D*	*P* ($D > 0$)	*P* ($D < 1$)
Native flora 1687–1689 vs. extirpated native species	705	0·85	<0·001	<0·001
Native flora 1687–1689 vs. native immigrants	732	0·76	<0·001	<0·001
Total flora 1687–1689 vs. non-native immigrants	845	0·62	<0·001	<0·001
Native flora 2000–2008 vs. threatened native species	729	0·73	<0·001	<0·001
Total flora 2000–2008 vs. potential future non-native immigrants	884	0·78	<0·001	<0·05

Discussion

We showed that over three centuries of urbanization – one of the main drivers of land conversion – plant species richness increased but phylogenetic richness and divergence decreased. This evolutionary loss is mainly driven by the non-random extirpation of phylogenetically unique native species and the immigration of phylogenetically non-random common native and non-native species. Although using not a strict temporal perspective, Winter *et al.* (2009) found a similar pattern of this loss of evolutionary uniqueness at country scale in Europe: increasing species richness but decreasing phylogenetic diversity. We showed that this non-random loss is likely to continue in the future with the loss of highly threatened plant species. Therefore, we argue that, even if there is no net change in species richness or even an increase in species richness at local or regional scales over time, like in our study or as recently shown for sites across the globe by Vellend *et al.* (2013) and Dornelas *et al.* (2014), we are losing and will so in the future another important facet of biodiversity (Cadotte, Dinnage & Tilman 2012).

We acknowledge ongoing discussions about the importance of phylogenetic diversity (Winter, Devictor & Schweiger 2013; Venail *et al.* 2015), but at the same time, evidence for its relevance is increasing (e.g. Staab *et al.* 2016). A loss of phylogenetic diversity is a loss of biodiversity per se and is likely to affect the stability of ecosystems (Cadotte, Dinnage & Tilman 2012) via the loss of general richness and of unique elements. However, we were not able to determine to what extent the loss of phylogenetic diversity that we found and expect to happen in Halle in the future will substantially affect ecosystems. We support the call for embracing existing uncertainties (Forest *et al.* 2015) and for actions to conserve phylogenetic diversity in times of intensive environmental alterations and biodiversity loss.

In response to the role of urbanization in biodiversity loss (Seto, Güneralp & Hutyra 2012), municipalities world-wide are increasing their conservation efforts. The Singapore Index on Cities' Biodiversity ('City Biodiversity Index'), for example, was developed from 2009 on to aid municipalities in assessing and evaluating their progress in biodiversity conservation (Convention on Biological Diversity 2009). Several cities published strategies on the protection of biodiversity (e.g., the Berlin Strategy for Biodiversity; Senatsverwaltung für Stadtentwicklung und Umwelt 2012) and the 'Cities and Biodiversity Outlook' (Secretariat of the Convention on Biological Diversity 2012) stressed the need to strengthen the conservation and sustainable use of urban natural resources. At the same time, designed urban green infrastructures are increasingly promoted in order to enhance the provision of ecosystem services and nature-based solutions (Kabisch *et al.* 2016).

While MacIvor *et al.* (2016) pointed out that the phylogenetic relationships of plant species should be considered

when designing urban green infrastructures, our results show that we have to especially focus our efforts on protecting threatened native species and their habitats in order to safeguard phylogenetic diversity. For the flora of Halle (the same data set as used here) and by using a functional approach, we had identified the habitat conditions related to extirpation in a previous study (Knapp *et al.* 2010). There, we found that extirpation was mainly driven by the loss of nitrogen-poor and cool habitats; developments that can be attributed to the vast anthropogenic input of nitrogen into Europe's ecosystems (Franzaring & Fangmeier 2006), the drainage of bogs for lignite mining (which in the Halle region had started in the 14th century and culminated in the 19th and 20th centuries; Walossek 2006), and increasing temperatures as a result of climate change and a growing urban heat island. A strikingly high number of today's threatened species which we analysed here – 46 of 74 species – is adapted to nitrogen-poor soils (e.g. *Adonis aestivalis* L., *Filago arvensis* L., *Inula germanica* L., *Orchis morio* L. or *Verbascum phoeniceum* L.; http://www.floraweb.de). Consequently, we can protect today's threatened species and their phylogenetic diversity by protecting nitrogen-poor, cool habitats. Such habitats will also serve human well-being (e.g. by regulating local temperatures) and should be considered when designing urban green infrastructures. Disentangling the importance of changing abiotic conditions (especially nitrogen concentration and temperature) and related changes in habitat composition for the development of phylogenetic diversity should be a focus of future urban biodiversity research (Fig. 3).

Similar to Čeplová *et al.* (2015) who (based on spatial data from 32 European cities) showed that phylogenetic diversity decreases with an increasing proportion of neophytes, we showed that, in the course of urbanization over three centuries, immigrating species added less phylogenetic diversity to urban floras than was lost with the extirpation of native species. Thus, although immigration can compensate for ongoing extirpation in terms of species numbers, it cannot compensate for the loss of phylogenetic diversity. Species that immigrate to urban areas are usually well-adapted to typical urban environmental conditions, such as high temperatures and high nitrogen loads (Knapp *et al.* 2010). Some of them, e.g. non-native tree species, are even discussed as potentially valuable for the design of climate-adapted urban green spaces (Gillner *et al.* 2016). To protect phylogenetic diversity in urban areas, planners should consider a phylogenetically rich and distinct set of species when designing green spaces.

We are well aware of the fact that we are generalizing the effects of urbanization on phylogenetic diversity based on one case study. However, we are convinced that Halle stands as a typical example with similar biotic and abiotic developments as in many other urbanized places. In the 17th century, the Halle region was dominated by agriculture. Likewise, world-wide, areas of high agricultural suitability became preferably urbanized, usually earlier than areas less well-suited for agriculture (Motamed, Florax & Masters 2014). Urbanization creates similar structures around the world, because urban areas are built for human needs (McKinney 2006). Consequently, urban environmental conditions are similar across the globe and similar drivers act on the extirpation of species, on the establishment of immigrating species and on changes in phylogenetic composition (Fig. 3). Measures to protect phylogenetic diversity will, thus, be transferable among cities. We suggest that these measures combine the
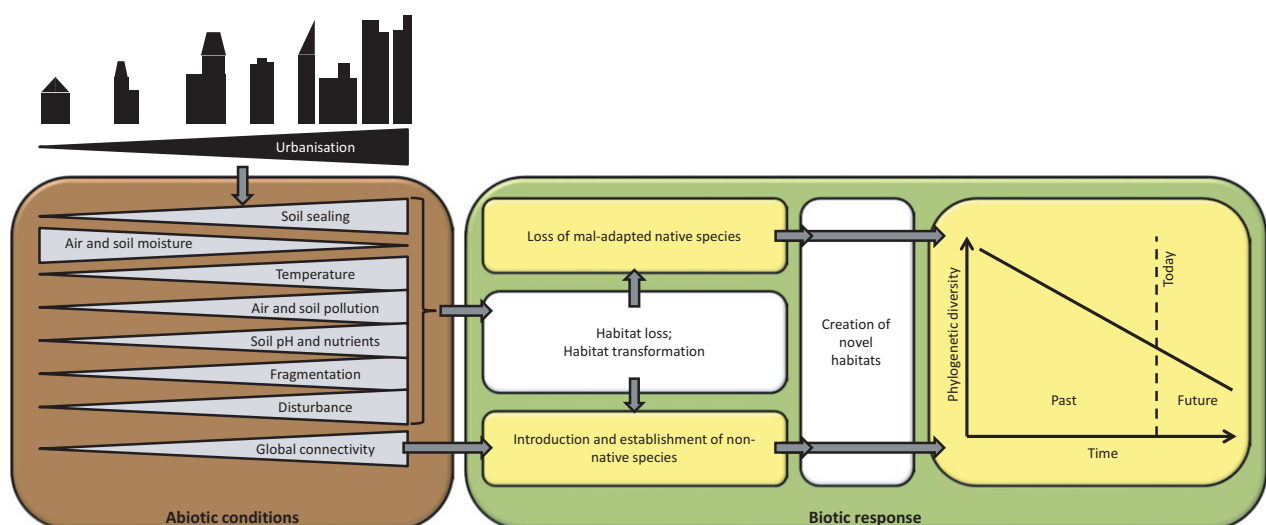
Fig. 3. Conceptual framework illustrating the interdependency of urbanization (black sketch), abiotic conditions (brown box) and biotic response (green box), with a focus on changes in species composition and related changes in phylogenetic diversity (yellow boxes). While the present study elucidates temporal changes in species composition and related changes in phylogenetic diversity, we argue that further research should disentangle how changes in abiotic conditions (and thus the underlying anthropogenic drivers) affect phylogenetic diversity. [Colour figure can be viewed at wileyonlinelibrary.com]

protection of threatened habitats and their species with the reduction of nitrogen loads and the creation and maintenance of green infrastructures that regulate urban temperatures. Maintaining 'cool urban habitats' such as shady forests will not only mitigate heat but also has the potential to safeguard evolutionary history.

Acknowledgements

Data accessibility

Species data (list of species used in the analyses with the time they were found in the study area and their native/non-native status) are archived as Supporting Information (Table S1), which may be found in the online version of this article. Phylogenetic data (Durka & Michalski 2012, 2016) are accessible at https://dx.doi.org/10.6084/m9.figshare.c.3305040.v1

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Table S1. Floristic data set used for the analysis of the phylogenetic composition of the flora of Halle (Saale), Germany, between 1687 and 2008, showing all species per time step with their native/non-native status according to BiolFlor (Kühn, Durka & Klotz 2004; http://www2.ufz.de/biolflor).

Table S2. Floristic inventories used for the analysis of the phylogenetic composition of the flora of Halle (Saale), Germany, between 1687 and 2008, divided into seven time steps.

Table S3. Number of vascular plant species in today's administrative district of the city of Halle (Saale), Germany, within the last 320 years, shown per time step with available plant records for (i) the total flora, (ii) the native flora and (iii) the non-native flora.

Table S4. Akaike's information criterion (AIC) for the comparison of models with time as predictor vs. intercept-only models.

Table S5. Development of species numbers from one time step to the next for (i) extirpated native species; (ii) immigrated native species; (iii) immigrated non-native species, including the sum from (i) to (iii) and the according ratio of immigrated to extirpated species.

Table S6. Phylogenetic richness of vascular plant species in today's administrative district of the city of Halle (Saale), Germany, within the last 320 years, shown per time step with available plant records and for (i) the total flora, (ii) the native flora and (iii) the non-native flora.

Table S7. Average phylogenetic distinctness of vascular plant species in today's administrative district of the city of Halle (Saale), Germany, within the last 320 years, shown per time step with available plant records and for (i) the total flora, (ii) the native flora and (iii) the non-native flora.

Fig. S1. Map of the study area.

Fig. S2. Phylogenetic tree of the flora of Halle (Saale), Germany.