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Floristic response to urbanization: Filtering of the bioregional flora in Indianapolis, Indiana, USA

Rebecca W. Dolan, Myla F.J. Aronson, and Andrew L. Hipp

PREMISE OF THE STUDY: Globally, urban plant populations are becoming increasingly important, as these plants play a vital role in ameliorating effects of ecosystem disturbance and climate change. Urban environments act as filters to bioregional flora, presenting survival challenges to spontaneous plants. Yet, because of the paucity of inventory data on plants in landscapes both before and after urbanization, few studies have directly investigated this effect of urbanization.

METHODS: We used historical, contemporary, and regional plant species inventories for Indianapolis, Indiana USA to evaluate how urbanization filters the bioregional flora based on species diversity, functional traits, and phylogenetic community structure.

KEY RESULTS: Approximately 60% of the current regional flora was represented in the Indianapolis flora, both historically and presently. Native species that survived over time were significantly different in growth form, life form, and dispersal and pollination modes than those that were extirpated. Phylogenetically, the historical flora represented a random sample of the regional flora, while the current urban flora represented a nonrandom sample. Both graminoid habit and abiotic pollination are significantly more phylogenetically conserved than expected.

CONCLUSIONS: Our results likely reflect the shift from agricultural cover to built environment, coupled with the influence of human preference, in shaping the current urban flora of Indianapolis. Based on our analyses, the urban environment of Indianapolis does filter the bioregional species pool. To the extent that these filters are shared by other cities and operate similarly, we may see increasingly homogenized urban floras across regions, with concurrent loss of evolutionary information.

Urban areas are surprisingly biodiverse, supporting a considerable number of vascular plant species (Aronson et al., 2014). Biodiversity contributes to a city's capacity to adapt to changing environmental conditions by maintaining ecosystem function (Díaz et al., 2006; Tzoulas et al., 2007; Haines-Young and Potschin, 2010). Diverse vegetation in cities provides ecosystem services such as air and water quality amelioration, flood retention, carbon sequestration, and climate regulation (Bolund and Hunhammar, 1999; Nowak et al., 2006; Manes et al., 2012; Gómez-Baggethun and Barton, 2013; Balvanera et al., 2014). A better understanding of how urban environments select for or against particular plant species would help in managing urban biodiversity, planning and executing sound ecological restoration, and predicting floristic responses to environmental change (e.g., Godefroid, 2001; Tait et al., 2005; Pavao-Zuckerman, 2008; Williams et al., 2009; Knapp et al., 2016).

Investigation of floristic change in response to urbanization is hampered, however, by the paucity of predevelopment floristic inventories (Stehlik et al., 2007; Knapp et al., 2016). Where data do exist, global trends have been difficult to identify. Seemingly simple questions, such as whether cities support more or fewer species across their geographic span than the area supported before urbanization, are complicated. Species numbers have been found to increase (McKinney, 2008), decrease (Goddard et al., 2010), or stay the same (Godefroid, 2001; Dolan et al., 2011a). Where species richness has not changed, there has often

been considerable turnover, with increases in nonnative species (e.g., Godefroid, 2001; Dolan et al., 2011a; Aronson et al., 2015). Varying results are based in part on whether the studies include only native species, spontaneous flora growing outside of cultivation, planted species, or all species. Additional confounding factors include global differences in regional species pools (La Sorte et al., 2014), age of cities (Aronson et al., 2014), and whether cities developed in areas already greatly altered by humans for agriculture or other purposes (Kühn and Klotz, 2006; Hahs et al., 2009).

An alternative to historical/current species presence comparisons is to substitute space for time, using inventories of transects or plots that span a range of contemporary development from rural through suburban, periurban to city centers (e.g., Sukopp, 2004; Kühn and Klotz, 2006; Wania et al., 2006; Lawson et al., 2008; Walker et al., 2009). Using this approach, urban floras have been shown to generally have greater species richness than surrounding rural areas (Wania et al., 2006; McKinney, 2008), because of increased numbers of both native and nonnative species (Sukopp, 2004) supported by the diverse habitats available in cities (Godefroid and Koedam, 2007; McKinney, 2008). This is especially true when planted species of gardens and landscaping are included (Williams et al., 2009). However, substituting space for time does not directly address the biotic processes that underlie changes in biodiversity (Knapp et al., 2016).

Another approach to understanding floristic change that accompanies urbanization is to examine shifts in plant functional traits. This approach moves beyond merely tabulating changes in species richness as a consequence of urbanization; rather, functional trait approaches seek to understand the features of plants that are selected by the urban environment (e.g., Godefroid, 2001; Lososovà et al., 2006; Knapp et al., 2009, 2010). Urban environments are known to filter bioregional floras (Williams et al., 2009); not every species found regionally can survive in cities. Habitat destruction, modification and fragmentation, continuous disturbance, soil compaction, and heat island effects are just a few of the factors that urban plants must tolerate (e.g., McKinney, 2008). Understanding how these factors interact to shape urban floras should allow prediction of species change with urbanization (Williams et al., 2009). However, a recent review of plant functional traits in 29 urban floras (Williams et al., 2015) found few consistent trends, highlighting the complexity of urban plant-environment interactions.

Phylogenetic approaches complement trait-based approaches to investigating the composition of urban floras. Because traits that adapt species to their environments evolve on the tree of life, phylogenetic diversity and phylogenetic distribution of taxa in a community are often informative about ecological interactions in and ecosystem functions of those communities (Cadotte et al., 2008; Knapp et al., 2012; Srivastava et al., 2012). Instead of using species' presence/absence counts or viewing species as composites of functional traits, phylogenetic approaches consider species as the endpoint of evolutionary history, organized hierarchically according to their ancestry.

Williams et al. (2009) predicted that urbanization would result in increased phylogenetic diversity of the flora because of the colonization of novel city habitats by exotic species. Where data exist, pre- and posturbanization comparisons make it possible to test whether species gains or losses with urbanization represent phylogenetically nonrandom filtering of the species pool and, if so, to infer which lineages may be preadapted to urban habitats. This approach has also been used to examine species changes along contemporary urbanization gradients. For example, phylogenetic diversity of spontaneous yard floras in Minneapolis, Minnesota, USA, did not change with housing density (a surrogate for urbanization), but yard species were more closely related to each other than were species from a nearby natural area (Knapp et al., 2012).

Additional studies are needed to identify plant traits or lineages that are favored or lost through urbanization (Thompson and McCarthy, 2008; Knapp et al., 2012; Williams et al., 2015) and to determine the degree to

which there are common characteristics of urban floras that stand out against the context of habitat differences among regions and variation in land use history (Kühn and Klotz, 2006; Knapp et al., 2016). By comparing historical data with recent inventories for the city of Indianapolis, Indiana, Dolan et al. (2011a) documented changes in species composition over time, including an increase of 7% in nonnative species, with an accompanying loss of 2.4 per year of native species, as well as extinctions—particularly of rare wetland plants. Native upland forest vegetation during the same interval persisted in parks and natural areas throughout the city (Dolan et al., 2011b). For our current study, we build on our understanding of changes in the flora of Indianapolis between 1940 and the early 21st century, a time during which the city increased in human population size and the built environment expanded. We characterize shifts in the phylogenetic relatedness and distribution of functional trait state frequencies among the same species by comparing plants present in the city now and the past with the bioregional flora, to document how the urban environment filters the species pool in time and space (e.g., Aronson et al., 2016). Finally, we examine trait and phylogenetic differences between native plants that persisted in the city's flora and those that were extirpated. Very few studies outside of Europe have addressed floristic changes in spontaneous flora associated with urbanization in a single city from the combined approaches of floristic composition, phylogenetic distribution, and functional traits.

MATERIALS AND METHODS

Background on Study Area

Indianapolis, Indiana, the twelfth largest city in the United States, is located in the midwestern part of the country in Marion County. It has an estimated population of more than 900,000 people and an area of 650 km² (105,200 ha). The city and the county are the same governmental unit and occupy the same geographic space, referred to as “Indianapolis” in this paper. The city is located in the Central Till Plain Section of the Central Till Plain Natural Region (Homoya et al., 1985). Indianapolis was almost entirely forested in pre-European presettlement times, but forest cover was reduced to 13% by the late 1900s (Barr et al., 2002); agriculture covered 80% of the landscape in 1922 (<http://www.savi.org>). Historically, mesic upland forest, mostly beech–maple association (Pötzger et al., 1956), covered 76% of the county, with small areas of drier upland forest on ridges. Wet-mesic depressional forests were scattered throughout the county with floodplain forests along major rivers and tributaries.

Floras and Taxonomic Analysis

The historical flora of Indianapolis before 1940 was compiled by Dolan et al. (2011a), based on published records (Deam, 1940) and specimens in the Friesner Herbarium (BUT; www.butler.edu/herbarium). That study also presented the contemporary flora based on recent (within the last 20 yr) inventories conducted around the city. These data constitute our current Indianapolis flora list. The USDA Plants Database (USDA NRCS, 2016) was used to compile the regional flora by downloading species records for Indianapolis/Marion County and all surrounding counties in the Tipton Till Plain Natural Region (i.e., Boone, Hamilton, Hancock, Hendricks, Johnson, Madison, Shelby, and Tipton). The county species lists obtained from USDA plants are based on herbarium records, as well as historic and current species lists from local-, regional-, statewide-, and national-species distribution references, and are constantly being updated (USDA NRCS, 2016). Taxonomy of species lists was standardized using the Taxonomic Name Resolution Service (2015; Boyle et al., 2013). To determine the beta diversity of the three floras (regional, historical Indianapolis, and current Indianapolis) based on presence and absence of species, we calculated Sørensen's distance (β_{sor}). We also calculated β_{sor} among the three floras based only on native species to examine the role of nonnative species in differentiating the floras.

Functional Trait Scoring and Analysis

For this study, 10 functional traits related to physiognomy, persistence, regeneration, pollination, and dispersal were scored for each taxon (Tables 1 and 2). All were categorical. Nativity was also scored and included in the trait analysis; while not a functional trait per se, nativity reflects a portion of the evolutionary history and the history of ecological interactions of the species. Traits were measured using modified versions of Cornelissen et al. (2003) and Pérez-Harguindeguy et al. (2013) standardized protocols for measurement of plant functional traits worldwide, adjusted to include only traits appropriate for the midwestern USA and those for which most plants had data in Gleason and Cronquist (1991)—the most recent comprehensive manual of the flora of Indiana and surrounding states. When data for a trait was not present in the manual, Internet sources listed in Appendix S1 (see the Supplemental Data with this article) were used.

We used χ^2 contingency tables to analyze differences in the frequency of functional trait states between the Indianapolis regional and current floras, between the current and historical floras, and between native plants that were present in both the historical and current floras (plants that survived) and native plants that were present historically, but are not in the current flora (plants that were extirpated). Analyses were performed using the Cross Tabulation function in Systat 12.0 (www.systat.com). Pearson χ^2 , Yates corrected χ^2 , and Fisher's exact test (needed when at least one tally value was less than five, i.e., a sparse cell in the tabulation) were used to establish significance levels. All gave the same results. We include only the Pearson χ^2 analysis.

Phylogenetic Data Preparation and Analysis

A phylogeny was assembled for the 846 species in our species list that were in the Zanne et al. (2014) phylogeny of more than 30,000 vascular plants; this was based on the genes 18S rDNA, 26S rDNA, ITS, matK, rbcL, atpB, and trnL-trnF. An additional 326 missing species from our species list were grafted onto the tree either at the crown node of their genus (294 species) or according to rules provided by us based on known phylogenetic or taxonomic relationships (32 species, Appendices S2 and S3). Pruning and grafting were conducted in R (R Core Team, 2016) using the 'ape' package (Paradis et al., 2004) and the `make.matAndTree` and `weldTaxa` functions of the Morton project (<https://github.com/andrew-hipp/morton>). Because polytomies and phylogenetic uncertainty introduced by welding taxa onto the base of genera may bias phylogenetic signal upwards (Davies et al., 2012), we generated 100 rarefied-to-genus trees of a single tip randomly selected per genus (517 tips), and conducted a subset of analyses on the rarefied-to-genus set of trees.

The phylogenetic distribution of species in the historical and contemporary Indianapolis flora was characterized using Purvis's D-statistic (Fritz and Purvis, 2010), which measures the degree of phylogenetic autocorrelation of a binary trait (in our case, present [1] vs. absent [0]). Because the difference between historical and contemporary floras may be strongly influenced by increases in nonnative species, we performed these analyses on the entire flora, as well as the native flora only, and reported both. The observed D-statistic for each analysis was compared to two null distributions: one simulated by random permutation of the tip states (P_{random}), and one simulated under a threshold model on a hidden Brownian motion process (P_{Brownian}) (Fritz and Purvis, 2010; Felsenstein, 2012). Phylogenetic diversity of the historical and contemporary Indianapolis flora was characterized using mean pairwise distance (MPD) and mean nearest taxon distance (MNTD) relative to a taxon-shuffling null. Again, analyses were conducted for the full taxon set and the natives-only taxon set; analyses were conducted in R using the 'caper' package (Orme, 2013) and the 'picante' package (Kembel et al., 2010).

Purvis's D-statistic (Fritz and Purvis, 2010) was used to investigate phylogenetic signal in three traits: the graminoid life form, the woody habit, and abiotic pollination mode. Because the difference between historical and contemporary floras may be strongly influenced by increases in nonnative species, we performed these analyses on the entire flora and the native flora only, and reported both. Traits were visualized on the phylogeny in R using the 'ggtree' package (Yu et al., 2016).

RESULTS

Approximately 60% of the current regional flora ($n = 1175$) was represented in the Indianapolis flora, both historically ($n = 699$) and currently ($n = 689$), but these species richness totals mask species turnover, because many species were present in only one time period. Beta diversity was similar across the three floras, with the historical and current floras having the greatest dissimilarity when including both native and nonnative species ($\beta_{\text{sor}} = 0.332$). The historical flora was more similar than the current flora to the regional flora ($\beta_{\text{sor}} = 0.237$ and $\beta_{\text{sor}} = 0.258$, respectively). Similar trends were seen when calculating beta diversity across the three floras with only native species. Dissimilarity between the historical flora and the current flora increased to $\beta_{\text{sor}} = 0.361$, showing that the introductions of nonnative species between the two time periods decreased beta diversity. The same trend was shown between the regional flora and the historical flora ($\beta_{\text{sor}} = 0.253$), as well as the regional and current floras ($\beta_{\text{sor}} = 0.260$).

Functional Traits

The composition of most functional traits was not significantly different among the three floras. Only one trait—pollination mode—differed between plants present in the current Indianapolis flora compared with the regional flora (Table 1). Plants with biotic pollination are highly significantly overrepresented, increasing in frequency by 6%, with a concomitant decrease in abiotic pollination.

Compared to Indianapolis' historical flora, the current flora has significantly more nonnative plants (28% vs. 22%) (Table 1). There are also significant differences in growth forms; more graminoids historically, and more forbs, trees, and shrubs currently. As in the regional vs. current city comparison, biotic pollination is also different between the two floras. There was a 7% increase in plants characterized by biotic pollination in the current compared with the historical flora.

More trait differences were detected between native plants that were survivors ($n = 381$), present in both the historical and the current flora, and those that were extirpated ($n = 164$), present in the historical flora, but not the current (Table 2). Here, growth form, life span, pollination, and dispersal were different between the floras. Aquatic plants and grasses decreased, while forbs were overrepresented among survivors. Therophytes (= annuals) tended to be lost, along with plants with abiotic pollination. Plants that persisted tended to be less likely to have unassisted dispersal, while animal-dispersed seed was overrepresented.

Phylogenetic Signal in Floristic Occurrence Data

The historical flora of Indianapolis samples randomly from the phylogeny of the regional flora for both the full suite of species ($D = 0.965$, $P_{\text{random}} = 0.097$), and the natives only ($D = 0.972$, $P_{\text{random}} = 0.169$) (Appendix S4). The current flora of the Indianapolis region, however, samples nonrandomly from the phylogeny of the regional flora whether the entire suite of species ($D = 0.843$, $P_{\text{random}} < 0.001$) or only native species are considered ($D = 0.833$, $P_{\text{random}} < 0.001$) (Fig.1, Appendix S4). This result holds on trees rarefied to genus (for all taxa, $D = 0.848 \pm 0.036$ SD; $P_{\text{random}} = 0.006 \pm 0.017$ SD). Nativity is very strongly phylogenetically structured ($D = 0.480$, $P_{\text{random}} < 0.001$). All tests conducted show less phylogenetic signal, however, than

expected if these were true traits evolving under a Brownian motion threshold model ($D > 0$, $P_{\text{Brownian}} < 0.001$).

TABLE 1. Frequencies of functional traits for the Indianapolis, Indiana, USA regional, historical, and current floras. χ^2 values test for differences from expected values based on the regional flora.

Category Trait	Regional Flora (<i>n</i> =1175)	Historical Flora (<i>n</i> =699)	Current Flora (<i>n</i> =689)	χ^2 Current vs. Historical	χ^2 Regional vs. Current
Nativity				8.76**	2.55
Native	0.757	0.784	0.723		
Exotic	0.243	0.216	0.276		
More than 1 value	0.001	0.000	0.001		
Growth Form				20.80*	1.41
Forb (Herb)	0.568	0.589	0.598		
Fern	0.022	0.021	0.020		
Grass,sedge,orrush	0.193	0.207	0.132		
Shrub	0.078	0.052	0.083		
Tree	0.060	0.069	0.090		
Succulent	0.003	0.003	0.004		
Vine (climber)	0.041	0.041	0.049		
Parasite	0.010	0.006	0.006		
Aquatic	0.017	0.009	0.010		
Other—more than 1 value	0.007	0.003	0.007		
Life Form				8.49	8.49
Phanerophytes	0.155	0.136	0.197		
Chamaephytes	0.014	0.014	0.013		
Hemicryptophytes	0.379	0.409	0.370		
Geophytes	0.212	0.197	0.210		
Therophytes	0.200	0.209	0.176		
Helophytes	0.020	0.024	0.022		
Hydrophytes	0.015	0.007	0.007		
More than 1 value	0.004	0.003	0.004		
Missing	0.001	0.000	0.000		
Life Span				4.45	4.45
Annual	0.153	0.165	0.126		
Biennial	0.023	0.024	0.029		
Perennial	0.747	0.730	0.766		
More than 1 value	0.077	0.082	0.078		
Clonality				0.58	0.06
Nonclonal	0.612	0.629	0.611		
Clonal aboveground	0.095	0.092	0.099		
Clonal belowground	0.288	0.273	0.286		
More than 1 value	0.003	0.003	0.003		
Missing	0.003	0.003	0.001		
Spinescence				0.09	0.00
No spines/thorns	0.938	0.943	0.939		
Spines/thorns	0.061	0.057	0.061		
Missing	0.001	0.000	0.000		
Leaf Periodicity				1.23	1.92
Evergreen leaves	0.019	0.019	0.028		
Deciduous leaves	0.969	0.969	0.961		
Semi-evergreen leaves	0.005	0.007	0.007		
More than 1 value	0.002	0.001	0.000		
Missing	0.005	0.004	0.004		
Dispersal Mode				11.64	11.29
Unassisted	0.422	0.441	0.382		
Wind	0.212	0.209	0.218		
Internal animal	0.151	0.129	0.179		
External animal	0.104	0.116	0.126		
Hoarding	0.015	0.017	0.026		
Water	0.035	0.031	0.026		
More than 1 value	0.059	0.001	0.044		
Missing	0.002	0.056	0.000		
Pollination				9.26*	8.21***
Abiotic	0.295	0.306	0.234		

Biotic	0.702	0.690	0.762
More than 1	0.000	0.000	0.001
Missing	0.003	0.004	0.003

* = $P < 0.05$.

** = $P < 0.01$.

*** = $P < 0.001$.

TABLE 2. Frequencies of functional traits for native plant species that either remained (=survived) in the flora of Indianapolis, or were extirpated, based on historical and current floras. χ^2 values test for differences in frequency between plants that remained and those that were lost.

Category Trait	Survived (<i>n</i> =381)	Extirpated (<i>n</i> =164)	χ^2
Growth Form			41.13***
Forb (Herb)	0.612	0.470	
Fern	0.029	0.024	
Grass, sedge, or rush	0.144	0.348	
Shrub	0.058	0.073	
Tree	0.100	0.018	
Succulent	0.000	0.006	
Vine (climber)	0.042	0.043	
Parasite	0.008	0.006	
Aquatic	0.005	0.012	
Other—more than 1 value	0.003	0.000	
Life Form			17.41*
Phanerophytes	0.181	0.091	
Chamaephytes	0.013	0.018	
Hemicryptophytes	0.417	0.433	
Geophytes	0.231	0.183	
Therophytes	0.118	0.226	
Helophytes	0.031	0.030	
Hydrophytes	0.005	0.012	
More than 1 value	0.003	0.006	
Life Span			9.31*
Annual	0.089	0.177	
Biennial	0.013	0.018	
Perennial	0.837	0.738	
More than 1 value	0.060	0.067	
Clonality			2.47
Nonclonal	0.003	0.646	
Clonal aboveground	0.583	0.073	
Clonal belowground	0.105	0.274	
More than 1 value	0.310	0.006	
Spinescence			0.27
No spines/thorns	0.955	0.945	
Spines/thorns	0.045	0.055	
Leaf Periodicity			2.24
Evergreen leaves	0.024	0.006	
Deciduous leaves	0.961	0.988	
Semi-evergreen leaves	0.010	0.006	
More than 1 value	0.005	0.000	
Dispersal Mode			22.27***
Unassisted	0.373	0.506	
Wind	0.220	0.171	
Internal animal	0.155	0.110	
External animal	0.131	0.061	
Hoarding	0.031	0.000	
Water	0.037	0.049	
More than 1 value	0.052	0.006	
Missing	0.000	0.098	
Pollination			12.54***
Abiotic	0.270	0.427	

Biotic	0.722	0.573
Morethan 1	0.005	0.000
Missing	0.003	0.000

* = $P < 0.05$.

*** = $P < 0.001$.

Phylogenetic diversity, as estimated using MNTD, increases from the historical to the contemporary Indianapolis flora in both the native species set (from 41.38, $P = 0.072$ to 47.15, $P = 0.704$) and in the full species set (from 35.06, $P = 0.036$ to 39.34, $P = 0.803$). An increase in MNTD means that the average phylogenetic distance from a species to its nearest neighbor in the contemporary is greater than the average distance in the historic flora, although the difference is not significant. Phylogenetic diversity, as estimated using MPD, shows little change from the historical to the contemporary Indianapolis flora, suggesting that there is no change in distance along the deepest nodes of the phylogeny: even if there is species turnover, there is not a systematic thinning of major clades from the historic to the present flora. No observed patterns in MPD/MNTD are significant after Bonferroni correction ($N = 6$ tests).

When mapped to phylogeny (Fig. 1), the trait data for native species revealed both the graminoid habit ($D = -0.550$, $P_{\text{Brownian}} < 0.001$, $P_{\text{random}} < 0.001$) and abiotic pollination ($D = -0.356$, $P_{\text{Brownian}} = 0.002$, $P_{\text{random}} < 0.001$) are significantly more phylogenetically conserved than expected under both the Brownian and the random null. The woody habit is indistinguishable from the Brownian null but significantly more clustered than expected under the random null ($D = -0.239$, $P_{\text{Brownian}} = 0.102$, $P_{\text{random}} < 0.001$). The same patterns are significant for the full suite of species (graminoid habit: $D = -0.510$, $P_{\text{Brownian}} < 0.001$, $P_{\text{random}} < 0.001$; abiotic pollination: $D = -0.305$, $P_{\text{Brownian}} = 0.004$, $P_{\text{random}} < 0.001$; woody habit: $D = -0.226$, $P_{\text{Brownian}} = 0.077$, $P_{\text{random}} < 0.001$).

DISCUSSION

Understanding which species are filtered from the regional species pool into cities sheds light on how cities affect assembly of urban floras (Aronson et al., 2016). The flora of a city is filtered directly from the regional species pool, including introduced species that are either broadly introduced or unique to the urban environment. The processes by which species in the regional pool are filtered by the cities' environments are just beginning to be understood. A taxonomic, functional, and phylogenetic approach, as taken here, allows us to understand the patterns by which species are filtered and infer processes driving the filtering of species. Our unique data set combines the regional, historical, and modern floras of the city of Indianapolis. Our analyses demonstrate that urbanization can increase taxonomic beta diversity and that the filtering processes in cities selects for certain clades that are defined in part by phylogenetically conservative traits, resulting in phylogenetically clustered floras.

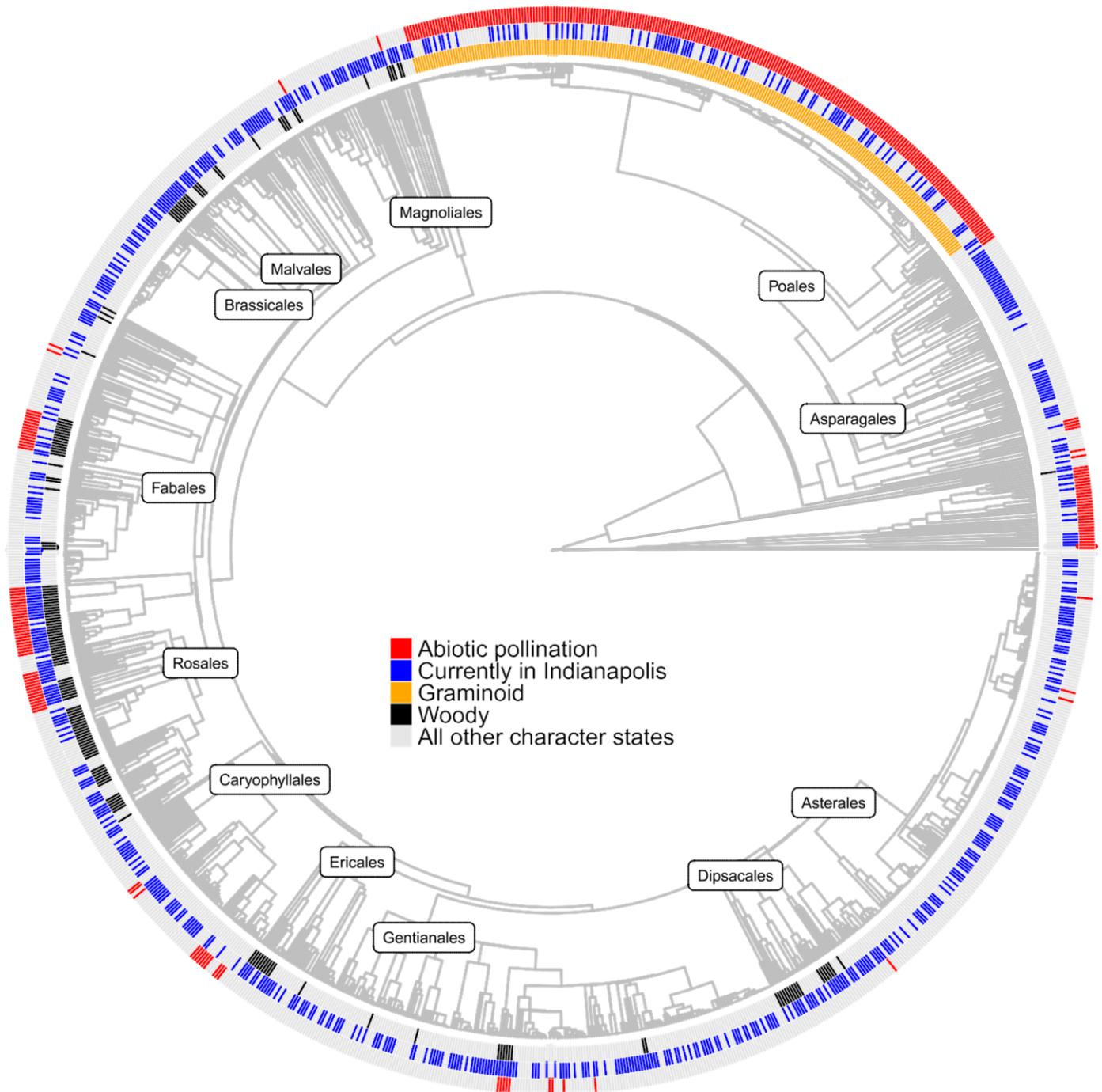


FIGURE 1 Phylogenetic distribution of two growth forms (graminoid and woody; orange and black bars respectively on the inner ring) and abiotic pollination syndrome (red bars; outer ring), which explain the phylogenetic signal in assembly of the contemporary Indianapolis flora, along with indication of which species in the regional flora are found in today's Indianapolis flora (blue bars; middle ring). Phylogeny with all tips labeled is presented in Appendix S3.

We found the highest beta diversity when comparing the current flora of Indianapolis to the historic flora. Differentiation between the current and historical floras increased when only natives were analyzed, indicating that the native species pool differentiates the floras, while the nonnatives have a homogenizing effect on beta diversity. Many studies have shown similar trends, attributing biotic homogenization to the extirpation of native species and the introductions of nonnative species (e.g., McKinney and Lockwood,

1999). Increases in urban land cover, loss of agricultural lands and natural habitats, and the introductions of nonnative species during urbanization are expected to homogenize city biotas when compared to rural areas (McKinney, 2008).

Patterns of functional trait state composition can provide insight into how the urban environment filters the regional flora (Knapp et al., 2008; Knapp et al., 2012; Aronson et al., 2016). For Indianapolis, there is a highly significant shift toward biotic pollination, when comparing both the regional and historic floras with the current flora. The current flora is composed of more trees and shrubs and fewer grasses than historically present. Dolan et al. (2011a) noted the largest physiognomic group added to the flora of Indianapolis over the last 70 years was ornamental shrubs escaped from cultivation. The increase in the current flora of plants pollinated by animals may reflect human preference for showy flowers and suggests cities may be good places for pollinators.

Native plants that persisted in the Indianapolis flora over the last 70 years tended to be perennials (geophytes and phanerophyte life forms) that are animal pollinated and animal dispersed. Extirpated plants were characterized as abiotically pollinated annuals with unassisted dispersal. These floristic changes occurred concomitantly with a landscape shift from agricultural fields to urban development. Agriculture cover decreased from 80% in 1922, to 18% in 1990 in Indianapolis (<http://www.savi.org>) while the human population doubled and urban/suburban land use increased. Many crop and pasture-land weeds are annuals (e.g., Lososová et al., 2006).

Our findings in some cases confirm former findings. Godefroid and Koedam (2007) and Knapp et al. (2010), for example, found increases in woody plants just as we did. However, our findings stand at odds with Knapp et al. (2008), who found less insect pollination with urbanization, and Palma et al. (2016) finding of increases in annuals. The discrepancy in our findings about insect pollination may have to do with the fact that graminoids decrease so strongly with urbanization in Indianapolis, and our temperate graminoids are all anemophilous. A recent review of 29 studies of plant functional traits in urban environments (Williams et al., 2015) found few consistent trends among cities, ascribing the result to variability in the consistency and strength of urban stressors and the importance of local factors. They describe urban plant environment interactions as complex, with many traits influenced by multiple disturbance effects. Comparisons among studies are complicated by the choice of traits studied and by limited information available on functional traits, such as seed mass and specific leaf area, for some floristic regions, including North America. Our results highlight the influence of the landscape matrix in which urbanization occurred (in our case a shift from an agricultural landscape to a built environment) on the species and traits able to persist in cities. This historical artifact of the landscape in which cities developed, e.g., urbanization on land that had already been converted from natural vegetation to agriculture, has been cited by others (e.g., Knapp et al., 2008 and Knapp et al., 2016) as strongly influencing direct floristic shifts following urbanization. Knapp et al. (2016) suggest their results for Halle, Germany may apply to other European cities with similar histories of land-use conversion. Likewise, our results should apply to other cities in the midwestern United States.

We show that the current Indianapolis flora is phylogenetically nonrandomly sampled from the regional species pool. Stated another way, the probability of a species passing through the urbanization filter is in part a function of its evolutionary history, its clade. Extinctions of phylogenetically distinct natives with an increase in phylogenetically common native and nonnative plants may cause such a trend (Knapp et al., 2016). This also suggests that the urbanization process in Indianapolis selects for phylogenetically constrained traits. In fact, we observe that this urbanization process selects against graminoids and for biotic pollination, both of which are phylogenetically conserved. Urbanization also selects for woodiness, which is restricted to a relatively small number of clades, with a preponderance of species in the rosids. Thus, the

phylogenetic filtering we observe in our study from the historical to the contemporary flora appears to be primarily a filtering of life form, which, in the case of graminoids, is linked to pollination mode.

Based on our analyses, the urban environment of Indianapolis filters the bioregional species pool, selecting for specific clades on the tree of life, limiting the plants that can grow in the city in ways not detected historically. To the extent that these filters are shared by other cities and operate in the same direction, homogenization of urban floras across regions and loss of evolutionary information may result (Knapp et al., 2016). Habitat heterogeneity within individual cities means they are not likely to be floristically homogenous (Kalusová et al., 2016), but urban floras are likely to become more homogenous regionally, resulting in cities that are less resilient to global climate change (Hahs and McDonnell, 2016). A better understanding of how plants respond to the novel habitats of cities is needed to help in planning for the future.

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DATA ACCESSIBILITY

Scripts and data used to conduct all phylogenetic analyses and create the phylogenetic figure are available at <https://github.com/andrew-hipp/indianapolis-flora-2017>.

Freely available online through the *AJB* open access option.

LITERATURE CITED

- Aronson, M. F. J., S. N. Handel, I. P. La Puma, and S. E. Clemants. 2015. Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. *Urban Ecosystems* 18: 31–45.
- Aronson, M. F. J., F. A. La Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, et al. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings. Biological Sciences* 281: 20133330.
- Aronson, M. F. J., C. H. Nilon, C. A. Lepczyk, T. S. Parker, P. S. Warren, S. S. Cilliers, M. A. Goddard, et al. 2016. Hierarchical filters determining community assembly of urban species pools. *Ecology* 97: 2952–2963.
- Balvanera, P., I. Siddique, L. Dee, A. Paquette, F. Isbell, A. Gonzalez, J. Byrnes, et al. 2014. Linking biodiversity and ecosystem services: current uncertainties and the necessary next steps. *Bioscience* 64: 49–57.

- Barr, R., C. B. E. Hall, J. A. Wilson, C. Souch, G. Lindsey, J. A. Bacone, R. K. Campbell, and L. P. Tedesco. 2002. Documenting changes in the natural environment of Indianapolis-Marion County from European settlement to the present. *Ecological Restoration* 20: 37–46.
- Bolund, P., and S. Hunhammar. 1999. Ecosystem services in urban areas. *Ecological Economics* 29: 293–301.
- Boyle, B., N. Hopkins, Z. Lu, J. A. Raygoza Garay, D. Mozzherin, T. Rees, N. Matasci, et al. 2013. The taxonomic name resolution service: an online tool for automated standardization of plant names. *BMC Bioinformatics* 14: 16.
- Cadotte, M. W., B. J. Cardinale, and T. H. Oakley. 2008. Evolutionary history and the effect of biodiversity on plant productivity. *Proceedings of the National Academy of Sciences, USA* 105: 17012–17017.
- Cornelissen, J. H. C., S. Lavorel, E. Garnier, S. Díaz, N. Buchmann, D. E. Gurvich, P. B. Reich, et al. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* 51: 335–380.
- Davies, T. J., N. J. B. Kraft, N. Salamin, and E. M. Wolkovich. 2012. Incompletely resolved phylogenetic trees inflate estimates of phylogenetic conservatism. *Ecology* 93: 242–247.
- Deam, C. C. 1940. Flora of Indiana. Department of Conservation, Division of Forestry, Indianapolis, Indiana USA.
- Díaz, S., J. Fargione, F. S. Chapin III., and D. Tilman. 2006. Biodiversity loss threatens human well-being. *PLoS Biology* 4: e277.
- Dolan, R. W., M. E. Moore, and J. D. Stephens. 2011a. Documenting effects of urbanization on flora using herbarium records. *Journal of Ecology* 99: 1055–1062.
- Dolan, R. W., J. D. Stephens, and M. E. Moore. 2011b. Living more than just enough for the city: persistence of high-quality vegetation in natural areas in an urban setting. *Diversity (Basel)* 3: 611–627.
- Felsenstein, J. 2012. A comparative method for both discrete and continuous characters using the Threshold Model. *American Naturalist* 179: 145–156.
- Fritz, S. A., and A. Purvis. 2010. Selectivity in mammalian extinction risk and threat types: a new measure of phylogenetic signal strength in binary traits. *Conservation Biology* 24: 1042–1051.
- Gleason, H. A., and A. Cronquist. 1991. Manual of the Vascular Plants of Northeastern United States and Adjacent Canada. 2nd edition. New York Botanical Garden, New York, New York, USA.
- Goddard, M. A., A. J. Dougill, and T. G. Benton. 2010. Scaling up from gardens: biodiversity in urban environments. *Trends in Ecology & Evolution* 25: 90–98.
- Godefroid, S. 2001. Temporal analysis of the Brussels flora as indicator for changing environmental quality. *Landscape and Urban Planning* 52: 203–224.
- Godefroid, S., and N. Koedam. 2007. Urban plant species patterns are highly driven by density and function of built-up areas. *Landscape Ecology* 22: 1227–1239.
- Gómez-Baggethun, E., and D. N. Barton. 2013. Classifying and valuing ecosystem services for urban planning. *Ecological Economics* 86: 235–245.

- Hahs, A. K., and M. J. McDonnell. 2016. Moving beyond biotic homogenization: searching for new insights into vegetation dynamics. *Journal of Vegetation Science* 27: 439–440.
- Hahs, A. K., M. J. McDonnell, M. A. McCarthy, P. A. Vesk, R. T. Corlett, B. A. Norton, S. E. Clements, et al. 2009. A global synthesis of plant extinction rates in urban areas. *Ecology Letters* 12: 1165–1173.
- Haines-Young, R., and M. Potschin. 2010. The links between biodiversity, ecosystem services and human well-being. In Raffaelli, D. G., and C. L. J. Frid [eds.] *Ecosystem ecology: A new synthesis*, 110–139. Cambridge University Press, Cambridge, UK.
- Homoya, M. A., D. B. Abrell, J. R. Aldrich, and T. W. Post. 1985. Natural regions of Indiana. *Proceedings of the Indiana Academy of Sciences* 94: 245–268.
- Kalusová, V., N. Čeplová, and Z. Lososová. 2016. Which traits influence the frequency of plant species occurrence in urban habitat types? *Urban Ecosystems* 20: 65–75.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornwell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* (Oxford, England) 26: 1463–1464.
- Knapp, S., L. Dinsmore, C. Fissore, S. E. Hobbie, I. Jakobsdottir, J. Kattge, J. King, et al. 2012. Phylogenetic and functional characteristics of household yard floras and their changes along an urbanization gradient. *Ecology* 93: S83–S98.
- Knapp, S., I. Kühn, J. P. Bakker, M. Kleyer, S. Klotz, W. A. Ozinga, P. Poschlod, et al. 2009. How species traits and affinity to urban land use control large-scale species frequency. *Diversity & Distributions* 15: 533–546.
- Knapp, S., I. Kühn, O. Schweiger, and S. Klotz. 2008. Challenging urban species diversity: contrasting phylogenetic patterns across plant functional groups in Germany. *Ecology Letters* 11: 1054–1064.
- Knapp, S., I. Kühn, J. Stolle, and S. Klotz. 2010. Changes in the functional composition of a Central European urban flora over three centuries. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 235–244.
- Knapp, S., M. Winter, and S. Klotz. 2016. Increasing species richness but decreasing phylogenetic richness and divergence over a 320-year period of urbanization. *Journal of Applied Ecology* 4: 1152–1160.
- Kühn, I., and S. Klotz. 2006. Urbanization and homogenization—Comparing the floras of urban and rural areas in Germany. *Biological Conservation* 127: 292–300.
- La Sorte, F., M. Aronson, N. Williams, L. Celesti-Gradow, S. Cilliers, B. Clarkson, R. W. Dolan, et al. 2014. Beta diversity of urban floras within and among European and non-European cities. *Global Ecology and Biogeography* 23: 769–779.
- Lawson, D. M., C. K. Lamar, and M. W. Schwartz. 2008. Quantifying plant population persistence in human-dominated landscapes. *Conservation Biology* 22: 922–928.
- Lososová, Z., M. Chytrý, I. Kühn, O. Hájek, V. Horáková, P. Pyšek, and L. Tichý. 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 69–81.

- Manes, F., G. Incerti, E. Salvatori, M. Vitale, C. Ricotta, and R. Costanza. 2012. Urban ecosystem services: tree diversity and stability of tropospheric ozone removal. *Ecological Applications* 22: 349–360.
- McKinney, M. L. 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems* 11: 161–176.
- McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14: 450–453.
- Nowak, D. J., D. E. Crane, and J. C. Stevens. 2006. Air pollution removal by urban trees and shrubs in the United States. *Urban Forestry & Urban Greening* 4: 115–123.
- Orme, D. 2013. The caper package: comparative analysis of phylogenetics and evolution in R. *R package version*, 5 (2). Available from: <https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf>.
- Palma, E., J. A. Catford, R. T. Corlett, R. P. Duncan, A. K. Hahs, M. A. McCarty, M. J. McDonnell, et al. 2016. Functional trait changes in the floras of 11 cities across the globe in response to urbanization. *Ecography* 40: 875–886.
- Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics (Oxford, England)* 20: 289–290.
- Pavao-Zuckerman, M. A. 2008. The nature of urban soils and their role in ecological restoration in cities. *Restoration Ecology* 16: 642–649.
- Pérez-Harguindeguy, N., S. Diaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. S. Bret-Harte, et al. 2013. New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany* 61: 167–234.
- Potzger, J. E., M. E. Potzger, and J. McCormick. 1956. The forest primeval of Indiana as recorded in the original U.S. land surveys and an evaluation of previous interpretations of Indiana vegetation. *Butler University Botanical Studies* 13: 95–111.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Srivastava, D. S., M. W. Cadotte, A. A. M. MacDonald, R. G. Marushia, and N. Mirotchnick. 2012. Phylogenetic diversity and the functioning of ecosystems. *Ecology Letters* 15: 637–648.
- Stehlik, I., J. P. Caspersen, L. Wirht, and R. Holderegger. 2007. Floral free fall in the Swiss lowlands: environmental determinants of local plant extinction in a peri-urban landscape. *Journal of Ecology* 95: 734–744.
- Sukopp, H. 2004. Human-caused impact on preserved vegetation. *Landscape and Urban Planning* 68: 347–355.
- Tait, C. J., C. B. Daniels, and R. S. Hill. 2005. Changes in species assemblages within the Adelaide metropolitan area, Australia, 1836–2002. *Ecological Applications* 15: 346–359.
- Taxonomic Name Resolution Service [Internet]. 2015. iPlant Collaborative. Version 4.0. [Accessed 28 August 2015]. Available from: <http://tnrs.iplantcollaborative.org>.
- Thompson, K., and M. A. McCarthy. 2008. Traits of British alien and native urban plants. *Journal of Ecology* 96: 853–859.

Tzoulas, K., K. Korpela, S. Venn, V. Yli-Pelkonen, A. Kaźmierczak, J. Niemela, and P. James. 2007. Promoting ecosystem and human health in urban areas using green infrastructure: a literature review. *Landscape and Urban Planning* 81: 167–178.

USDA NRCS. 2016. The PLANTS Database. National Plant Data Team, Greensboro, NC 27401-4901 USA.

Walker, J. S., N. B. Grimm, J. M. Briggs, C. Gries, and L. Dugan. 2009. Effects of urbanization on plant species diversity in central Arizona. *Frontiers in Ecology and the Environment* 7: 465–470.

Wania, A., I. Kühn, and S. Klotz. 2006. Plant richness patterns in agricultural and urban landscapes in Central Germany. *Landscape and Urban Planning* 75: 97–110.

Williams, N. S. G., A. K. Hahs, and P. A. Vesk. 2015. Urbanisation, plant traits and the composition of urban floras. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 78–86.

Williams, N. S. G., M. W. Schwartz, P. A. Vesk, M. A. McCarthy, A. K. Hahs, S. E. Clemants, S. E. Corlett, et al. 2009. A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology* 97: 4–9.

Yu, G., D. K. Smith, H. Zhu, Y. Guan, and T. Tsan-Yuk Lam. 2016. ggtree: an r package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* 8: 28–36.

Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlinn, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506: 89–92.