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Rebecca W. Dolan
Butler University, rdolan@butler.edu

Marcia E. Moore
Butler University

Jessica Stephens
Auburn University Main Campus

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Rebecca W. Dolan, Marcia E. Moore, and Jessica D. Stephens

Friesner Herbarium and Center for Urban Ecology, Butler University, Indianapolis, IN 46208, USA
Department of Biological Sciences, Auburn University, Auburn, AL 36849, USA

Abstract

1. As human populations increasingly live in cities, urban floras and the ecosystem services they provide are under increasing threat. Understanding the effects of urbanization on plants can help to predict future changes and identify ways to preserve biological diversity. Relatively few studies document changes through time in the flora of a focal region and those that do primarily address European floras. They often rely on contemporary spatial gradient studies as surrogates for changes with time.
2. We compare historical species records (prior to 1940) with the current flora for Marion County, Indiana, USA, home to Indianapolis, the 13th largest city in the United States. Specimens from the Friesner Herbarium of Butler University and other vouchered records for the county provided the basis for historical records. Current records are derived from inventories of 16 sites conducted by Herbarium staff and other botanists over the past 15 years.
3. Physiognomic group, wetland classification and nativity (native vs. non-native) were determined for each species. Fidelity to high-quality habitat was quantified using coefficients of conservatism (C-values).
4. The last 70 years have seen a significant turnover in species presence, most notably a decrease in native plant species number (2.4 per year) and quality, with an accompanying increase in non-native plants of 1.4 per year. Loss of species has been non-random, with a disproportionate number of high-quality wetland plants lost. The signature of past land use can be seen in physiognomic changes in the composition of the flora that reflect the shift from agriculture to urban/suburban land use.
5. Many invasive non-native shrubs now present have escaped from cultivation, highlighting the combined threats of habitat conversion and human plant preference to native flora in cities. These invasives likely present the greatest threat to remaining biodiversity.
6. *Synthesis*. This study demonstrates the value well-documented historical records, such as those housed in herbaria, can have in addressing current ecological issues.

Introduction

It is estimated that for the first time in history more than half of the world's people now live in cities (UNFPA 2007). Urbanization puts great pressure on natural resources needed to provide ecosystem services to support burgeoning human populations. Likewise, urban green spaces are becoming important refuges for native biodiversity (Goddard, Dougill & Benton 2009). At the same time, the social importance of urban floras has never been greater (Stenhouse 2004; Fuller *et al.* 2007). In the coming decades, most people's contact with nature will be in urban settings (Thompson & McCarthy 2008).

The emerging field of urban ecology seeks to explore, document and understand the functioning of ecosystems in intimate association with humans and the built environment (Kaye *et al.* 2006; Shochat *et al.* 2006; Shen *et al.* 2008). A growing body of literature supports the notion that generalizations from studies of ecosystem processes in natural systems may not be applicable in human-dominated systems (Williams *et al.* 2009). For example, urban sites have altered disturbance regimes (Sukopp 2003) resulting in a perpetual state of disequilibrium. Theories of stability based on equilibrium are likely to be inadequate for urban ecosystems (Rebele 1994). Intentional and unintentional introductions of non-native species have degraded habitats and shift community composition in urban settings in ways that influence delivery of ecosystem services and habitat resiliency (Niinemets & Penuelas 2008; Walker *et al.* 2009). Finally, resource availability for co-evolved fauna, such as pollinators and seed dispersers, are likely to be greatly altered by urbanization (Burghardt, Tallamy & Shriver 2009).

Despite its potential to generate significant change, as noted by Tait, Daniels & Hill (2005), relatively few studies have investigated the effects of urbanization on flora. Studies examining biodiversity and richness of urban floras have typically found reduced overall biodiversity (Goddard, Dougill & Benton 2009) but greater species richness than surrounding rural areas (Wania, Kuhn & Klotz 2006; McKinney 2008). These results are usually attributed to the increased numbers of both native and non-native species (Sukopp 2003), most likely caused by cities having larger species pools due to landscaping and gardening (Walker *et al.* 2009). Also, both species types are able to occupy the diverse habitats available in cities, with their heterogeneous landscapes, compared with more homogeneous agriculture-dominated rural areas (Rebele 1994; Wania, Kuhn & Klotz 2006; Godefroid & Koedam 2007; McKinney 2008).

In addition to spatial patterns, it is important to investigate how urbanization has affected floras through time. Several studies examining temporal effects of urbanization on flora have used transect data that document changes that span the rural–urban gradient (e.g. Sukopp 2003; Lawson, Lamar & Schwartz 2008; Walker *et al.* 2009). With this approach, contemporaneous spatial patterns are surrogates for change with development over time. A few studies have examined the relationship between plant species' functional traits and their success at persisting in urban areas (e.g. Godefroid 2001; Chocholoušková & Pyšek 2003; Knapp *et al.* 2009, 2010). However, additional information describing changes in urban floras through time is still needed to better guide sound ecological restoration and management (e.g. Godefroid 2001; Tait, Daniels & Hill 2005; Pavao-Zuckerman 2008) and to predict future changes.

The paucity of studies that directly compare historical floras in formerly less urbanized areas with the current flora present in the same area (Stehlik *et al.* 2007) is due to lack of comprehensive historical data for most cities. In this article, we compare vouchered historical records from 1905 to 1940 of plant species occurring outside of cultivation in Marion County, Indiana, USA, with contemporary inventories to document changes in the flora. Using herbarium specimens, collections of pressed and dried plants that document flora of a region, we provide a record of floristic changes through time in response to urbanization. We hypothesized that land use changes would be reflected in: (i) an increase in the total number of species due primarily to an increase in non-natives resulting from spread of weedy species and escapees from gardens and landscaping; (ii) the loss of species with preference for high-quality natural habitat (due to direct effects of habitat destruction and indirect effects of fragmentation and alteration of natural disturbance regimes; (iii) shifts in physiognomy due to changes in habitat availability and community composition and (iv) possible phylogenetic shifts in species composition in response to landscape pattern changes and changing evolutionary selective pressures with urbanization.

Materials and Methods

The Friesner Herbarium of Butler University (BUT) was founded in 1919 and contains over 42,000 specimens collected in Indiana. Over 2800 of these were collected in Marion County, home to the university and the city of Indianapolis, which has served as the state capital since 1831. Marion County has the largest population of any county in the state, an estimated 900,000 people. There are an estimated one million more in the surrounding counties that make up the greater Indianapolis metropolitan area. Marion County is currently one of the 20 most populated counties in the United States with a total area of approximately 1050 km^2, its human-population density of 857 inhabitants km^{-2} is considered very high (http://www.citydata.com) by United States standards.

Marion County is located in central Indiana, in the Central Till Plain Section of the Central Till Plain Natural Region (Homoya *et al.* 1985). General Land Office Survey records witness trees from 1820 to 1822 and soil survey records indicate that Marion County was 98% forested in pre-European settlement times (Barr *et al.* 2002), with remaining land cover being open water or prairie. Mesic beech–maple upland forest covered 76% of the county, with small areas of oak–hickory forest on drier ridges. Wet–mesic depressional forests were scattered throughout the county with floodplain forests along major rivers and tributaries. Wetlands including ponds, bogs, marshes and fens are estimated to have made up approximately 1% of the original land cover (Barr *et al.* 2002). Barr *et al.* (2002) reported recent forest cover in Marion County reduced to 13% by the late 1900s. In 1922, an estimated 80% of land use was agriculture (http://www.savi.org). Agricultural use remained consistent through 1953 at 72%, but rapid urbanization in the 1960s and 1970s reduced the amount of farmland by half; by 1990, only 18% remained.

Published historical records for Marion County were compiled and nomenclature was updated to follow the USDA Plants Database (http://plants.usda.gov). Deam's authoritative 1940 *Flora of Indiana* (Deam 1940) reports records by county for species for which he confirmed vouchers in herbaria. These records were checked against 2820 specimens deposited at BUT and additional sheets in the Deam Herbarium at Indiana University (IND). Historical collection localities within the county were also gathered from specimens in each collection.

While herbarium specimens provide a concrete and reviewable record of plants growing in a particular place at a particular time, there are caveats to be aware of when using them to establish historical floras. They tend not to be uniform in location and habitat description, as noted by Fuentes *et al.* (2008). However, in the label convention used at BUT, all sheets have county of collection specifically listed, and county boundaries have been in place in central Indiana since 1816. Level of collection effort can bias data gleaned from herbarium specimens and presents particular challenges when, for example, using herbarium specimens to track the spread of non-native species across landscapes by decade (e.g. Delisle, Lavoie & Lachance 2003 or Lavoie, Dufresne & Delisle 2005). We categorize our species into just two groups, historical (pre-1940) and recent (since 1996), reducing the likelihood of bias. Marion County specimens at BUT were not collected in a systematic method and may not cover all habitats and geographic regions in the county. However, they represent the efforts of 28 different collectors, beginning in 1905. We assume this broad coverage reduces chances of pseudo-absences, where species were present but either not encountered or collected and therefore not documented.

Recent records were compiled from surveys of 16 sites conducted by the authors and students from BUT from 1996 to 2009, covering over 8.5 km^2, along with a few surveys provided by other botanists. Most locations inventoried were parks with significant natural area remaining, but habitats of all disturbance levels are included. Three are State Dedicated Nature Preserves. The areas recently inventoried cover approximately 8% of the county's non-mowed vegetated area and approximately 80% of forested remnants (Barr *et al.* 2002). Vouchers documenting recorded species for four sites are deposited at BUT. Recent records for non-native species include the observational records of Overlease & Overlease (2007). It is difficult to know how comprehensive these recent studies are compared with historical records and collections. There is less remnant natural habitat remaining, which would tend to concentrate effort, but there are also more second-growth woods in the county where agriculture has been abandoned.

We used coefficients of conservatism (C-values) to quantify species' fidelity to high-quality habitats and therefore, tolerance of disturbance, as an indicator of overall floristic quality. C-values were chosen for analysis of our data because they are comprehensive for the plants in our study area, provide a numerical value for species' behavior, and can be used to make statistical comparisons between sites and through time. C-values, originally devised for the flora of the Chicago region by Swink & Wilhelm (1994), rank native species from 0 to 10 based on fidelity to high-quality habitats, with higher numbers indicating greater preference for high-quality habitat and less tolerance of disturbance. Because habitat characteristics and species behavior often vary geographically, C-values must be assigned at a regional scale. In 2004, C-values were assigned to all the species known to grow in Indiana by a panel of nine experts with great familiarity with the state flora (Rothrock 2004). C-values are now available for at least six state floras and one Canadian province and their use is gaining wide acceptance among land managers and restoration ecologists (Rothrock 2004). They have been used to identify high-quality remnant habitat (e.g. Rothrock & Homoya 2005; Ruch *et al.* 2007) and to quantitatively track the habitat quality of restorations through time (usually several years) based on the species they support (e.g. Taft, Hauser & Robertson 2006; McIndoe *et al.* 2008). To our knowledge, ours is the first study to use C-values to track floristic changes over decades.

C-values for species present in Marion County historically and those seen in recent surveys were compiled and analysed, along with species' nativity, physiognomy and wetland type indicator using Floristic Quality Assessment software developed by the Conservation Research Institute (Wilhelm & Masters 2004). The software assigns each species a regional numeric 'wetness' value corresponding to U.S. Fish and Wildlife Wetland Category type (http://plants.usda.gov/wetinfo.html). Obligate wetland species score −5, obligate upland species 5. Plants listed as native are those considered to have been present in Indiana at the time of western European settlement. We include only plants growing spontaneously, outside of cultivation (native and naturalized).

Results

Comparison of the contemporary flora of Marion County with historical records shows both reporting about 700 species (Table 1). The percentage of non-native species has increased from slightly more than 20% to over 27%. Mean C-value for native species did not change with time, but there has been a significant decline in mean C-values with non-natives included (given C-values of zero) (Table 1).

Table 1 Floristic quality data comparing historical records of Marion County, Indiana, USA, with recent inventories

	Historical	Recent
Total species	706	698
No. native species	563	509
Percentage non-native	20.3	27.1
Native mean C	4.2	4.0
Native mean C with non-natives	3.4*	2.9
Native mean wetness	0.2	0.4

*Significantly different at $P < 0.01$ based on nonparametric *t*-test using Wilcoxon rank-sum test with continuity correction

Although there has not been much of a change in overall species richness, there has been considerable species turnover. Thirty-one percent of all species reported historically have not been seen during recent studies. Eighty-eight percent of these are native species, which equates to a loss of 2.4 native species per year. Additions to the flora almost balance losses. Two hundred and eleven species have been seen in recent studies that were not reported by Deam (1940), representing 30% of the current flora. Almost half of these, 96 of 211, are non-native plants. This equates to a rate of non-native species gain of 1.4 per year.

Historical records report 54 more species of native plants than have recently been seen (Table 2). Native perennial forbs are the most common physiognomic group for both time periods, accounting for almost 50% of species. Recent inventories show notable decreases in annual forbs, perennial and annual grasses and perennial sedges. More native trees and shrubs have been reported in recent years than were reported historically.

Table 2 Comparison of the physiognomic breakdown of species of native and non-native plants reported historically with contemporary inventories in Marion County, Indiana, USA

	Native species Historical			Recent		
	Total	(%) Total*	(%) Native†	Total	(%) Total*	(%) Native†
No. species	563	79.7	—	509	72.9	—
Tree	50	7.1	8.9	58	8.3	11.4
Shrub	31	4.4	5.5	34	5.0	6.9
Woody vine	13	1.8	2.3	14	2.0	2.8
Herbaceous vine	6	0.8	1.1	7	1.0	1.4
Perennial forb	259	36.7	46.0	253	36.2	49.7
Biennial forb	17	2.4	3.1	14	2.0	2.8
Annual forb	60	8.5	10.7	45	6.4	8.8
Perennial grass	38	5.4	6.7	25	3.6	4.9
Annual grass	14	2.0	2.5	5	0.7	1.0
Perennial sedge	53	7.8	9.4	34	4.9	6.7
Annual sedge	7	1.0	1.2	5	0.7	1.0
Fern	15	2.1	2.7	14	2.0	2.8
	Non-native species Historical			**Recent**		
	Total	(%) Total*	(%) Non-native‡	Total	(%) Total*	(%) Native‡
No. species	143	20.3	—	189	27.1	—
Tree	3	0.4	2.0	11	1.6	5.8
Shrub	1	0.1	0.7	23	3.2	11.6
Woody vine	2	0.3	1.4	4	0.6	2.1
Herbaceous vine	0	0.0	0.0	1	0.1	0.5
Perennial forb	43	6.0	30.1	62	8.9	32.8
Biennial forb	16	2.3	11.1	21	3.0	11.1
Annual forb	48	6.8	33.6	47	6.7	24.9
Perennial grass	17	2.4	11.9	14	2.0	7.4
Annual grass	13	1.8	9.1	7	1.0	3.7
Perennial sedge	0	0.0	0.0	0	0.0	0.0
Annual sedge	0	0.0	0.0	0	0.0	0.0
Fern	0	0.0	0.0	0	0.0	0.0

*Percentage of total species (native and non-native)
†Percentage of native species only
‡Percentage of non-native species only

The distribution of species with different C-values (range 0–10) indicates a loss of species indicative of high-quality remnant habitat based on C-value (C-values 8–10) (Fig. 1). Losses of species with C-values of 10 and 9 were most dramatic, with shifts from 14 to two and seven to one respectively (Table 3). Almost all of these plants are obligate wetland species with wetness values of −4 or −5.

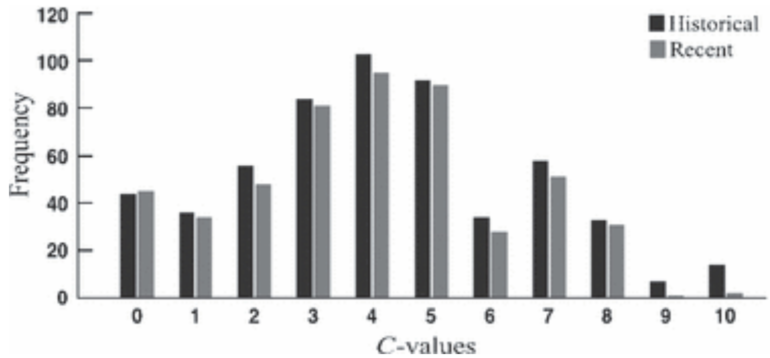

Figure 1 Number of species for each C-value reported for the Marion County, Indiana, USA, flora in historical and recent studies

Table 3 Species in the Marion County, Indiana, USA, flora with C-values of 9 and 10

Scientific name	C	w	Historical	Recent
Acorus americanus	10	-5	x	
Carex bromoides	10	-5	x	
Carex lupuliformis	10	-4	x	
Cornus amomum	10	-4	x	
Deschampsia caespitosa	10	-4	x	
Dryopteris cristata	10	-5	x	
Dulichium arundinaceum	10	-5	x	
Eleocharis erythropoda	10	-5	x	
Eleocharis ovata	10	-5	x	x
Lysimachia hybrida	10	-5	x	
Melanthium virginicum	10	-5	x	
Sagittaria rigida	10	-4	x	
Saxifraga pensylvanica	10	-5	x	
Symphyotrichum laeve	10	5		x
Ulmus thomasii	10	-1	x	
Carex careyana	9	5	x	
Comarum palustre	9	-5	x	
Cystopteris bulbifera	9	-2	x	
Diplazium pycnocarpon	9	1	x	x
Filipendula rubra	9	-4	x	
Helianthus microcephalus	9	4	x	
Triphora trianthophora	9	4	x	

w refers to species habitat preferences. Wetness value and ranges from -5 for obligate wetland species to 5 for obligate upland species.

Perennial forbs and grasses are the largest groups of non-native plants in both historical and recent records (Table 2). The most notable shifts in the physiognomy of non-natives with time are very large increases in woody species (Table 4). The number of trees increased from three to 11 and the number of shrubs increased from one to 23. There was also a large decrease in the percentage of annual forbs and grasses.

The number of non-native herbaceous invasive species in Marion County has increased only slightly since the time of Deam (1940) (Table 5). Fourteen species considered 'most unwanted' invasive plants by the Indiana Cooperative Agricultural Pest Survey Program (http://extension.entm.purdue.edu/CAPS/) based on the threats they pose to cultivated and natural plant communities have been seen in recent surveys. Only two of these are new to the flora: *Alliaria petiolata* (M. Bieb.) Cavara & Grande and *Humulus japonicus* Siebold & Zucc. were not reported by Deam for Indiana in 1940. *Phalaris arundinacea* L. was known from elsewhere in Indiana but not reported for Marion County by Deam, indicating it is not new to the region. *Dipsacus laciniatus* L., *Glechoma hederacea* L. and *Melilotus officinalis* (L.) Pall. were known for the county as early as 1895 (Wilson 1895).

Table 4 Woody non-native species reported in recent studies of the Marion County, Indiana, USA, flora

	Scientific name
Shrubs	*Berberis thunbergii**‡§¶
	Elaeagnus umbellata¶
	Euonymus alatus¶
	Euonymus fortunei¶
	Fallopia japonica¶
	Frangula alnus¶
	Hydrangea paniculata
	Ilex opaca§
	Ligustrum obtusifolium¶
	Ligustrum vulgare¶
	Lonicera maackii¶
	*Lonicera morrowii**‡¶
	Lonicera tatarica§¶
	*Lonicera ×bella**‡¶
	Phlox subulata
	*Rhamnus cathartica**‡¶
	Rhodotypos scandens
	Robinia hispida§
	Rosa multiflora§¶
	Rubus idaeus var. idaeus§
	*Viburnum lantana**‡
	Viburnum opulus var. oplulus‡
	Vinca minor†‡¶
Trees	*Acer platanoides*¶
	*Ailanthus altissima**‡
	*Alnus glutinosa**‡§
	Catalpa bignonioides
	Cotinus coggygria‡
	*Elaeagnus angustifolia**‡
	Maclura pomifera‡
	*Morus alba**‡
	Pinus sylvestris
	*Salix alba**‡
	Ulmus pumila¶
Woody vines	*Celastrus orbiculatus*¶
	Hedera helix¶
	Lonicera japonica§¶
	Solanum dulcamara‡

†Planted by city Parks Department in 1912, 1914 and/or 1915.
*Reported by Wilson (1895)
‡Reported by Deam (1940) for Marion County.
§Reported elsewhere in Indiana by Deam
¶Considered an invasive non-native landscaping plant by the Midwestern Invasive Plant Network and the Invasive Plant Species Assessment Working Group (http://www.mipn.org).

Table 5 Invasive non-native herbaceous species found in historical and recent floristic survey in Marion County, Indiana, USA

Scientific name	Historical	Recent
Alliaria petiolata		x
Bromus inermis	x	x
Cirsium arvense	x	x
Coronilla varia	x	x
Dipsacus laciniatus	x	x
Euphorbia escula	x	x
Glechoma hederacea	x	x
Hesperis matronalis	x	x
Humulus japonicus		x
Lysimachia nummularia	x	x
Lythrum salicaria	x	x
Melilotus officinale	x	x
Ornithogalum umbellatum	x	x
Phalaris arundinacea	x	x

The plants historically known from Marion County are from 106 families. Recent inventories have identified plants from 113 families. Nearly a third of the flora during both inventory times belongs to one of three families. For both historical and contemporary inventories, Asteraceae are the most common family comprising about 12.6 and 13.6% of plants respectively. Poaceae (11.0 and 7.3%) and Cyperaceae (8.6 and 5.5%) are second and third in abundance during both sample times. The distribution of species among plant families, an indicator of taxonomic evenness, did not change appreciably with time (Fig. 2).

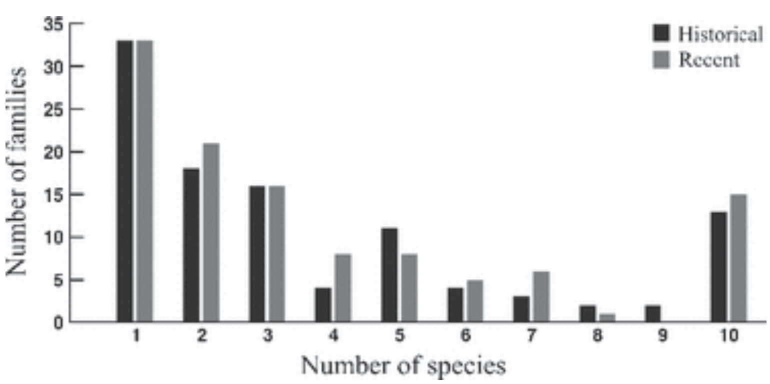

Figure 2 Distribution of species among families for plants reported for the Marion County, Indiana, USA flora in historical and recent studies.

Discussion

Total Species Richness

We predicted landscape changes brought about through urbanization would result in an increase in species richness in Marion County, but both historical and recent inventories yielded about 700 species, albeit with considerable species turnover with time. This number is lower than the 1300 species average for European cities of over 1 000 000 inhabitants reported in Zerbe *et al.*

(2004) and is actually in the range they report for cities with between 100,000 and 200,000 people. We did not include ornamentals or other plants growing in cultivation, which may account for our lower number. It may also be that central Indiana's flora is relatively depauperate overall due to its fairly recent post-glacial history (glaciers covered the northern two-thirds of the state as recently as 11 000 years ago) (Rothrock & Homoya 2005) and prominent till plain soils with few specialized edaphic types.

Although overall numbers of species have remained constant, there has been an increase in the number of non-native species. When mean C-values, with and without non-natives, vary by more than 0.7 units, natural quality is likely to have been compromised by the presence of the non-natives (Rothrock & Homoya 2005). For species listed by Deam (1940), mean C-values with and without non-natives differ by 0.8 units; for recent studies the values differ by 1.1 units. These values suggest an increasing negative impact on the quality of the flora by the presence of non-natives. Our results are similar to those of Godefroid (2001) for a study of changes to the flora of Brussels, Belgium, with urbanization. While the number of species remained constant from 1943 to 1994, based on inventories of 187 1-km^2 grids that covered the city, there was considerable turnover with an increase in the number of non-native species from 12–20%.

Several studies have used comparisons of historical and contemporary flora of urban areas to look at the relationship between plant species' functional traits and their success at persisting in cities. Throughout Germany, plants in cool habitats or on acidic soils are at the greatest threat from urbanization (Knapp et al. 2009), while through time the flora of Brussels, Belgium, is becoming more nitrophilous and tolerant to shade and heat (Godefroid 2001). Knapp *et al.* (2010) found that between 1687 and 2008, about 22% of the flora turned over in the city of Halle, Germany. Analysis of the functional composition of the species revealed that plants of nitrogen-poor habitats, plants of bogs and plants with helomorphic leaves were more likely to go extinct, while species dispersed by humans, those preferring nitrogen-rich conditions, warm habitats and mesomorphic leaves were more likely to be overrepresented by successful non-natives.

Rural and agricultural lands are generally assumed to have less biodiversity than wildlands due to habitat loss, alteration and increased homogeneity (Shochat *et al.* 2006). Biodiversity, measured as number of species, can rebound when urbanization occurs due to increased heterogeneity of habitat types available in cities (Godefroid & Koedam 2007; McKinney 2008) and increased species pools (Williams *et al.* 2009). This recovery in species number is, however, usually due to increases in non-native and less desirable species with lower fidelity to high-quality habitat. Our results support this trend for Marion County, with considerable species turnover in the last 70 years, with loss of native species being largely balanced by increases in non-natives.

Non-Native Species Composition

The most notable shift in non-native species composition in our study is the increase in trees and shrubs (Table 4), most of which are considered invasive. Almost all of the woody non-natives that are now present growing outside of cultivation in the county are landscape species introduced through the horticultural trade. Records of the Indianapolis Parks Department list many of these species in Marion County as selected for planting along parkways in the city in the 1910s (Board of Park Commissioners 1919) (Table 4). Thus, efforts to beautify the city early in the century have left a legacy of invasive species that the city's parks department stewardship office now spends much of its annual budget to eradicate.

Escape of woody non-native plants from landscaping reflects a cultural and social impact on urbanizing floras (Godefroid & Koedam 2007; Knapp *et al.* 2010) and may be a general trend. Woody non-native plants also increased significantly over 120 years in a case study of urban flora in the Czech Republic (Chocholouškovà & Pyšek 2003) increasing from two in 1910, to eight in the 1960s, to 33 by the 1990s. The city of Adelaide, Australia, experienced a greater than 100% increase in non-native tree species, with no loss of native trees between 1836 and 2002 (Tait, Daniels & Hill 2005).

Native Species Composition

Native mean C-values of 4.2 for species mentioned in Deam (1940) and 4.0 for recent studies are in line with values for published studies of less urbanized areas of the Central Till Plain Natural Region, which averages mean C-values of 4.1 (Rothrock & Homoya 2005). Values in the range of 4 indicate species are typically associated with remnant plant communities that are tolerant of significant to moderate disturbance (Rothrock 2004).

Indianapolis was built in the last century in a mostly agricultural matrix. Development of cities in more pristine areas is predicted to result in greater loss of native plants than development in former agricultural landscapes that have already been greatly disturbed (Preston 2000). However, we found a 10% reduction in native species over time, so extirpation continued in the American Midwest during the last century, even as the percentage of land devoted to agriculture decreased.

We predicted alteration and loss of high-quality habitat would result in loss of high C-value native species in Marion County. Species with C-values of 9 or 10 (species considered to be restricted to remnant landscapes that appear to have suffered very little post-settlement trauma) have greatly declined between census periods, with local extinction of most plants with C-values of 10, confirming our predictions. Plants extirpated tended to be wetland species. Records of specimen collection sites from BUT and IND show four of these plants were collected from only a single wetland site that was destroyed in the 1950s. Stehlik *et al.* (2007), in a study of species loss over time in Swiss lowlands, found wetland plants suffered greater species loss than plants of other habitats. Drainage of bogs in Halle, Germany, is cited by Knapp *et al.* (2010) as a major driver of species extirpation in that city. Our results also support the more general finding of

Duncan & Young (2000) in their study of extinction and rarity over 145 years for the flora of the city of Auckland, New Zealand: initially rare species were the most likely to be extinct or rare at the end of the time period.

The rate of loss of native species from the Marion County flora over the last 70 years is larger than that reported in few other studies that have compared historical floras with contemporary floras. Our observed rate of loss of native species of 2.4 per year is greater than the estimate of 1.7 and 2.0 for Middlesex and Cambridgeshire in England since 1750 (Preston 2000), 1.3 for species in a conservation area in metropolitan Boston from 1894 to 1993 (Drayton & Primack 1996) or 0.7 in the city of Auckland, New Zealand, from 1871 to 1985 (Duncan & Young 2000).

Physiognomic Shifts

Land use changes from agriculture to urban and human choice can be significant drivers of species turnover with urbanization (Knapp *et al.* 2010). Physiognomic shifts in the vegetation of Marion County in the last 70 years reflect changing land use patterns, as predicted. The decline of farmland may be the cause of the large decrease in the percentage of native and non-native annual forbs along with a drop in native annual and perennial grasses. Many crop and pasture land weeds, both native and non-native, are annuals (e.g. Lososovà *et al.* 2006). The large increase in woody non-native plants, as discussed previously, is due to escape of ornamental plants from yards and commercial landscaping.

Phylogenic Shifts

Finally, we predicted phylogenetic shifts in species composition in response to changing selective pressures that accompany urbanization. Plants can respond quickly to such changes. At the species level, the annual weed Crepis sancta has been shown to respond to urban sidewalk habitat within 12 generations by genetic alteration of dispersal mode (Cheptou et al. 2008). Adaptations that promote long-distance dispersal in this species are selected against in favour of non-dispersing seeds when suitable habitat is fragmented and the likelihood of successful dispersal reduced. Our analysis of plant family composition as an indicator of shifting evolutionary selective pressures did not find evidence of changes in Marion County in the last 70 years.

Conclusions

Williams *et al.* (2009) present a framework for understanding floristic changes in response to urbanization based on factors that influence habitat availability, spatial arrangement of habitats, the pool of plant species and evolutionary selective pressures on population persistence. They identify four filters: (i) habitat transformation, (ii) fragmentation, (iii) the urban environment and (iv) human preferences. Our data indicate urbanization in Marion County has clearly been influenced by two of these filters. High-quality wetland species have been locally extirpated due to habitat loss and changing patterns of land use have shifted the physiognomic composition of plant communities and species that comprise them. The species pool has also been greatly influenced by human preference for non-native landscape shrubs, which have now escaped from cultivation.

Urbanization can also be seen as a local extinction filter (Williams *et al.* 2005). Our finding of loss of high-quality wetland plants adds to a small set of urban flora studies that document this connection. Larger and more representative studies are needed to help determine the strength of different filters, to further identify plant and habitat traits that are favoured or lost through urbanization (Williams *et al.* 2005; Thompson & McCarthy 2008; Knapp *et al.* 2010) and to determine the degree to which there are common characteristics of urban floras that override regional habitat differences and past land use. Herbarium collections, with their documentation of species' historical presence, will continue to be an important resource for future studies in urban ecology.

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