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A COMPARATIVE BIOGEOGRAPHY OF THE VASCULAR FLORAS OF ILLINOIS AND INDIANA

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ABSTRACT. A symposium on γ biodiversity and the natural history collections of Illinois and Indiana was held at the 2017 annual meeting of the Indiana Academy of Science and included an analysis of the biogeography of the vascular plant floras of these two states. The analysis documented a rich temperate zone flora: the species shared by the two states numbered 2540 and a total count of 3450 species (native and non-native). Although the two states have much in common physiographically, on a per $\log_{10}$ km^2 basis Illinois possesses the richer flora. Illinois has at least 360 native species in its flora that do not occur in Indiana while only 165 species are limited to Indiana. The richer Illinois flora was due to a larger influence by the Great Plains flora, larger numbers of species reaching their northern limit in the Mississippi Embayment, more species reaching their southern limits especially within the Driftless Area of Illinois, and elements of the Ozark flora reaching into southern and western Illinois. Furthermore, at least 58 species introduced into Illinois (but not into Indiana) have a nativity from western US. Although Indiana has a notable Appalachian component in its flora, these deciduous forest species tend to also be found in the southern Illinois hill country. However, unique to Indiana was a suite of coastal plain disjunct species with populations in northwestern Indiana and also southwestern Michigan.

Keywords: Illinois, Indiana, biogeography, plant biodiversity

INTRODUCTION

For the past 125 years botanists have actively sampled the floras of Illinois and Indiana, amassing in excess of a half million herbarium specimens. This work has resulted in the compilation and publication of state floras by Mohlenbrock (1st edition 1975; 4th and most recent edition 2014) for Illinois and Charles Deam (1940) for Indiana. In addition, a major floristic series, started by Floyd Swink, documented the floristically diverse Chicago region (Swink 1969; Swink & Wilhlem 1994; Wilhelm & Rericha 2017).

These floras not only recorded the species of plants growing spontaneously within these two states, they also provided insight into the phytogeography of this region of the Midwest and a defining of natural regions (Schwegman et al. 1973; Homoya et al. 1985). The natural boundaries often have a physiographic basis including glacial history, bedrock type, and proximity to Lake Michigan. In addition there is a moisture gradient that, along with fire, drove historic vegetation to include expanses of tallgrass prairie and oak savanna in addition to eastern deciduous forest (Omernik & Griffith 2014, EPA 2017).

The Indiana Academy of Science at its 2017 annual meeting sponsored a two-state biodiversity and natural history collections symposium. For the first time, a broad range of organism groups, including mammals, invertebrates, plants, and fungi, was analyzed for their γ diversity (Whittaker 1972) across the two states. The two states have much in common physiographically. Both have glaciated as well as unglaciated regions and both have a long north–south axis resulting in a diverse mix of species from cooler and warmer climes. Likewise both have large river systems (Illinois, Mississippi, Ohio, and Wabash) with extensive bottomlands as well as frontage on Lake Michigan. At the same time, the two-state analysis, especially for plants, revealed some unexpected differences in their floras and faunas. In this paper, the Venn diagram approach is used to ask which vascular plant species are in common between the two states and which are unique to each and to explore potential causation behind these patterns.

MATERIALS AND METHODS

Species lists for Illinois and Indiana were compiled from Biota of North America Project (BONAP, Kartesz 2017), a database that treats the two states and nearby regions in a similar manner (but see Franz & Sterner (2017) for cautions related to aggregated biodiversity databases overall). In Microsoft's Access® database,

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species in common across the Illinois and Indiana were sorted and enumerated. Each remaining species was scored for state occurrence, nativity, and a series of phytogeographic range limits. The latter were determined through the study of species distribution maps found in Kartesz (2017). In particular, these maps provided information on which species reached their northern or southern range limit in each state, which reached their eastern limit in Illinois or western limit in Indiana, which had disjunct distributions (i.e., outlier populations in Illinois or Indiana widely separated from the species' center of distribution), and which could be defined as regional endemics. Two forms of regional endemism were defined: those of limited geographical range from the Ozark Mountain region into Illinois and the second centering on the Interior Low Plateau that lies between the Appalachian range and Mississippi River floodplain and extends from southern Indiana to northern Alabama.

RESULTS AND DISCUSSION

Whittaker (1972) envisioned three levels of species diversity: α diversity is the richness of species at the community level, β diversity is species turnover along habitat gradients, and γ diversity is the total diversity of a landscape or geographical area. The latter may be thought of as a product of α and β diversity. Thus, the following interstate floristic comparisons largely fall into the category of γ diversity. An estimated 3450 species (2594 native species) are found in the two-state region (Table 1), with a larger number of plant species known for Illinois (3283) than for Indiana (2865). Illinois, in fact, had more native species (2429) than any of the states or province examined including Indiana. Indiana was more species-rich than several more northern states (Wisconsin and especially Minnesota) and comparable in richness with Michigan and Kentucky (Table 1). The greater species richness of Illinois compared to Indiana could be attributed to the larger size of the former and, on an unscaled species/km^2 basis, Indiana does indeed seem more species rich. However, when scaled on either a semilog (Table 1) or log-log basis (not shown) basis, as is typical for species-area relationships (Connor & McCoy 1979), several interesting trends emerge. The historically prairie states of Kansas and Iowa had the fewest native species per unit area. Likewise more northern states (Minnesota, Wisconsin) and the province of Ontario had low numbers of species. Species richness often correlates with factors such as ecosystem productivity, precipitation, and temperatures (e.g., Bai et al. 2007; Wang et al. 2009). Based upon the $\log_{10}$ km^2 calculation, Illinois has 471 native species per unit area compared to only 439 for Indiana, i.e., Illinois enjoys a 7% advantage over Indiana.

Illinois and Indiana share 2540 species in common. Indiana has 230 species not known from Illinois, about 8% of its flora (Table 2). In contrast, the Illinois flora has an estimated 680 species unknown in Indiana or more than 20% of its species list. Since these values are for all vascular plant species, whether native or non-native, it could be that these differences reflect a more thorough monitoring of recent introductions. In part this is true. Nonetheless the pattern

Table 1.—Number of vascular plant species known for Illinois, Indiana, and neighboring regions. Data based upon BONAP (Kartesz 2017). SR = species richness; SR_total = species richness of native + non-native species.

State or Province	SR_total	SR_native	Native_SR/km^2	Native_SR/$\log_{10}$ km^2
Illinois	3283	2429	0.017	471
Indiana	2865	2180	0.023	439
Illinois + Indiana	3450	2594	0.011	483
Iowa	2274	1733	0.012	336
Kansas	2302	1808	0.008	339
Kentucky	2899	2191	0.021	437
Michigan	3099	2207	0.015	422
Minnesota	2398	1863	0.009	351
Missouri	3026	2262	0.012	429
Ohio	3146	2213	0.019	437
Ontario	3336	2382	0.002	395
Pennsylvania	3567	2408	0.020	476
Wisconsin	2698	2005	0.014	390

Table 2.—Number of vascular plant species unique to Illinois versus Indiana.

	Illinois	Indiana
Unique native + non-native species	680	230
Unique native species	360	165
Unique native species per $\log_{10}$ km^2	69.8	33.2

persists when comparisons are made with native species only (Table 2), which are well known for both states. Most telling was that on a per $\log_{10}$ km^2 basis, Illinois had 70 unique native species per unit area compared to only 33 for Indiana.

The data suggest that Illinois has a greater endowment of plant species. An exploration of biogeographical patterns might provide clues as to why this is the case. First, to-date Illinois does have a larger number of introduced species that are not recorded for Indiana. Interestingly, 58 of these Illinois introductions are from the western US and 11 from southern US. Indiana has only nine introduced species from other portions of the US that are not also recorded for Illinois. Unpublished work by Kay Yatskievych (pers. comm.), however, is rapidly enlarging the list of introduced species in Indiana. These have not been analyzed for their co-occurrence in Illinois.

Each state possesses a unique suite of species that have a relatively narrow geographic range overall. Southern and western Illinois has about 12 regional endemics that collectively display an Ozark influence. Example species include *Ruellia pedunculata* Torr. ex A. Gray and *Symphyotrichum anomalum* (Engelm.) G. L. Nesom. Indiana on the other hand has approximately three regional endemics whose distribution is limited to the Interior Low Plateau: *Carex picta* Steud., *Hypericum dolabriforme* Vent., and *Viola egglestonii* Brainerd. *Solidago shortii* Torr. ex A. Gray, a species whose narrow distribution consists of one site on the Indiana side of the Ohio River and three Kentucky counties, could be included on this list. Two additional species were not included as Indiana regional endemics. *Eleocharis bifida* S. G. Sm. has unresolved taxonomic questions and may be an undescribed species. *Physaria globosa* (Desv.) O'Kane & Al-Shehbaz has its sole and ecologically puzzling Indiana station in the Wabash River Valley rather than on the Interior Low Plateau.

Table 3.—Number of species reaching their range limit in either Illinois or in Indiana.

	Illinois	Indiana
Species reaching their northern limit	97	29
Species reaching their southern limit	51	23
Species reaching their eastern limit (in Illinois) or western limit (in Indiana)	56	27

The greater geographical reach of Illinois, compared to Indiana, both to the south as well as the north, accounts in part for that state having more species that attain their north–south limit (Table 3). Illinois has 97 species that reach their northern limit compared to Indiana's 29. Species such as *Nyssa aquatica* L. extend northward up the Mississippi Embayment from the coastal regions into southern Illinois and often do not make it into Posey County in the extreme southwestern corner of Indiana. At the opposite end of these two states, 51 northern species have occurrences in northwest Illinois. This is the Driftless Area, unglaciated during the most recent glacial maximum, and home to species such as *Gymnocarpium dryopteris* (L.) Newman (Pusateri et al. 1993). The Driftless Area also harbors *Dodecatheon amethystinum* (Fassett) Fassett and *Solidago sciaphila* Steele, species with narrow geographic range globally that are limited to dolomite and sandstone cliffs and talus slopes (Pusateri et al. 1993).

An analysis of species reaching their eastern and western range limits again reveals greater numbers of species for Illinois. *Astragalus crassicarpus* Nutt. and 55 other species of the Great Plains flora reach into Illinois but have not been observed in the limited area of tallgrass prairies of presettlement western Indiana. Conversely only 27 species, such as *Lilium canadense* L., have their western limit in Indiana. By and large it appears that those elements of the Appalachian flora whose range extends as far west as Indiana also have found suitable habitat in the southern Illinois hill country.

One suite of species sharply favors Indiana over Illinois, the so-called coastal plain disjunct species. Indiana has at least 12 species with a bimodal distribution pattern in which the center of distribution is along the Atlantic and Gulf of Mexico coastal plain and a distinct secondary center near the end of Lake Michigan. Example

species include *Eleocharis melanocarpa* Torr. and *Xyris difformis* Chap. Due to the quirks of postglacial geology, sand dune formation, and placement of the state line, Illinois has no coastal plain species that do not also occur in Indiana.

In summary, both Illinois and Indiana have richer floras than more northern states, Ontario, and the prairie-dominated states such as Kansas and Iowa. The flora of Indiana, while rich and interesting, is on a par with neighboring states of Kentucky, Michigan, and Ohio, and, aside from a suite of coastal plain disjunct species, supports fewer biogeographically limited species than its neighbor state to the west. On the other hand, Illinois has a remarkably rich vascular flora, i.e., high γ diversity. This stems in part from a confluence of privileged geography and geological history, such as observed by Ricklefs & He (2016). Illinois' high γ diversity may be attributable to its long north–south axis, its pattern of glaciation, and the influence of the Ozark flora. In addition, the state straddles two biomes, so that prairie species are abundant and yet Appalachian and floral elements of the deciduous forest biome also are abundant. Thus, one might envision that the state has high species turnover or high β diversity across the biome transition zone (Kark & vanRensburg 2006). As more historic and current herbarium records become available in digital databases (e.g., see midwestherbaria.org), it should be possible to address interesting species distributional questions across transition zones and how these zones are changing in response to climatic shifts and the influx of non-native species.

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