IN THIS ISSUE

One of the strengths of this journal is a long history of floras of natural areas, such as parks and preserves, throughout the Great Lakes region. Many of these include descriptions and analyses of the plant communities in such natural areas as well as floristic quality assessments. Taken together, these articles provide an important snapshot of the current floristic status of the region as well as a baseline for further research. The study in this issue by Ryne Rutherford and Susan Fawcett of the Seven Lakes Nature Preserve in Michigan's Upper Peninsula is an important contribution to this series. The area consists of aquatic, wetland, and upland habitats in a highly intact area that is now preserved by a private conservation organization. Several new county records were encountered during this study.

Pitcher's Thistle, *Cirsium pitcheri*, a favorite of many naturalists in the western Great Lakes region, is also an imperiled species of Great Lakes shorelines and has long been the subject of ecological studies. This issue presents the second such study in three years to appear in these pages (the first was in the July–December 2021 issue, Volume 60, Nos. 3–4). The present article examines the effect of age of flowering on the survivorship and fecundity of this monocarpic species (a species that lives for several years but flowers only once), which especially for a rare species, has implications for conservation, recovery, and adaptability to climate change.

Continued exploration of Michigan's Upper Peninsula continues to reveal surprises. The Noteworthy Collections article in this issue reports new records of glade fern, *Homalosorus pycnocarpos*, and expanded woodfern, *Dryopteris expansa*, for the eastern portion of the Upper Peninsula.

This issue concludes with a review of a fascinating and well-illustrated volume exploring the various strange and unusual ways that members of the orchid family have adapted to animal-dependent pollination, with particular emphasis on deception and reward strategies.

——Michael Huft

VASCULAR PLANT COMMUNITIES AND FLORA OF THE SEVEN LAKES NATURE PRESERVE IN MICHIGAN'S EASTERN UPPER PENINSULA

Ryne Rutherford[1]
Michigan Technological University
U.J. Noblet Forestry Building
1400 Townsend Drive, Houghton, MI 49931-1295
Biophilia, LLC, 32104 W State Highway M-64, Ontonagon, MI 49953.

Susan Fawcett
University and Jepson Herbaria, University of California, Berkeley
1001 Valley Life Sciences Building, Berkeley, CA 94720.

ABSTRACT

The Seven Lakes Nature Preserve comprises nearly 2,400 hectares of aquatic, wetland, and upland habitats in southeastern Alger and northeastern Schoolcraft counties in the eastern Upper Peninsula of Michigan. The preserve was obtained and protected by the J.A. Woollam Foundation and has undergone several expansions. In an area of Michigan with relatively limited development and few roads, the natural communities of Seven Lakes are highly intact, and many of its habitats have recovered since the historic logging era. Botanical surveys were conducted in 2016, 2017, 2020, 2021, and 2022 with the goals of describing the natural communities and ecosystem processes and of producing a comprehensive floristic inventory. The post-glacial natural history of the region and a description of climate and soils are provided. A floristic quality assessment was performed, yielding a Total Floristic Quality Index of 99.9, a Total Mean C of 4.5 and a Native Mean C of 5.3. Within the upland forests, shrubby and forested wetlands, and open wetlands, eleven plant communities are described following the classification system proposed by the Michigan Natural Features Inventory. The floristic affinities of rare or otherwise noteworthy taxa are discussed, as are potential threats to the ecosystem. Four-hundred ninety-three species and four hybrids were observed during our surveys, 147 species are represented by specimen vouchers and 440 are recorded as photo vouchers on iNaturalist. Sixteen new species records for Alger County are reported.

KEYWORDS: Floristic Inventory, Great Lakes, Floristic Quality Assessment, Natural Communities

INTRODUCTION

The Seven Lakes Nature Preserve (Seven Lakes) (Figure 1) comprises nearly 2,400 hectares of aquatic, wetland, and upland habitats in southeastern Alger and northeastern Schoolcraft counties in the eastern Upper Peninsula of Michigan. In an area of Michigan with relatively limited development and few roads, the natural communities of Seven Lakes are highly intact, and many of its habitats have recovered since the historic logging era. Botanical surveys were conducted in

---

[1] Author for correspondence (biophilianature@gmail.com).

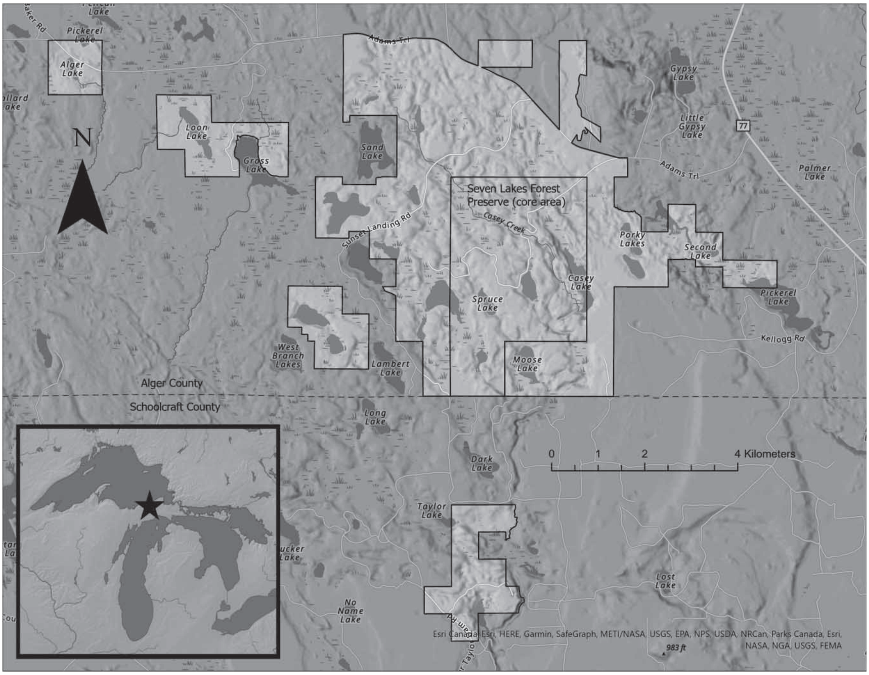

FIGURE 1. Map of the Seven Lakes Nature Preserve in southeastern Alger and northeastern Schoolcraft Counties, Michigan. All areas of the Nature Preserve are in lighter shading. The Seven Lakes Forest Preserve (core area) is indicated. The other tracts on the map outside the core area are known collectively as Seven Lakes Forest Reserve.

2016, 2017, 2020, 2021, and 2022 with the goals of describing the natural communities and ecosystem processes and of producing a comprehensive floristic inventory.

Southeastern Alger and northeastern Schoolcraft counties in the northeastern Upper Peninsula of Michigan have been understudied by ecologists until recent years. Situated nearby well-known places such as Pictured Rocks National Lakeshore to the north and west, Seney National Wildlife Refuge to the south, and Tahquamenon Falls State Park to the east, Seven Lakes and the area directly adjacent to the preserve consists of sparsely visited privately owned timberland. A private conservation organization, the J.A. Woollam Foundation, has taken great interest in this area and currently owns Seven Lakes. Founded in 2000, the mission of the J.A. Woollam Foundation is to help protect undeveloped land and the plants and animals that occur there. They support land trusts and conservation groups with similar interests. Beginning in 2016, the J.A. Woollam Foundation contracted Biophilia, LLC to conduct multi-taxa ecological surveys of the property which is divided into two management units. The Seven Lakes Forest Preserve is the core of the property and is exempt from timber harvest; it comprises 557 hectares. Beyond the core area is the Seven Lakes Forest Reserve, comprising 1,786 hectares, which is subject to occasional timber harvest outside of wetland buffer zones. The property and survey area consists of one large parcel, and four smaller parcels to the south and west.

The climate in Alger and Schoolcraft counties is categorized as Dfb = warm summer humid continental climate by the Köppen–Geiger Classification system (Kottek et al. 2006). According to the Midwestern Regional Climate Center (MRCC), monthly average temperature (1981–2010) at the nearest station with long-term weather data, Munising, Michigan (45 km to the WSW of Seven Lakes), ranges from –7.8°C (17.9°F) in January to 18.2°C (64.8°F) in July, with an annual average of 6.4°C (42.0°F) (MRCC 2021). The average growing season is 140 days near Lake Superior and fewer than 100 days inland. Average yearly precipitation is between 81 and 86 cm, and annual snowfall is as high as 457 cm in the highlands near Lake Superior (Albert 1995). Situated between 270 and 300 meters in elevation, Seven Lakes is higher than the surrounding lacustrine-influenced terrain of the eastern Upper Peninsula and around 100 meters higher in elevation than Lake Superior. Seven Lakes is in a unique geographic position, sitting at the headwaters of the Fox River in the Lake Michigan watershed, yet much closer to Lake Superior, which is only 8 to 18 kilometers away. Although snowfall amounts are not measured for this exact location, they are reported to be among the highest in the region by local residents (John Herman, personal communication). The lacustrine influenced temperature moderation and precipitation, including snow lingering long into spring, forms a unique mesic climate.

The entire area comprising Seven Lakes is underlain by 500-million-year-old Cambrian age sandstone, which is not directly exposed at the surface but comes close along the Fox River in the southern portion of the preserve near the Alger-Schoolcraft County border. The bedrock is overlain by a variety of glacial deposits, which may be up to 65 meters thick, and which were deposited during the Wisconsin glaciation at the end of the Pleistocene epoch 9,000–12,000 years ago (LaBerge 1994). Coarse-textured glacial till caps some of the higher morainal ridges, while pitted outwash dominates much of the lower portions of Seven Lakes. The pitted outwash plains contain many kettle lakes, bogs, and other wetlands. Peat deposits in bogs are several meters deep in places and can occupy just a few hectares, while others are tens of hectares in size. Poorly to extensively drained sands surround the wetlands, and podzols are the dominant soil type in the area. Soils in the upland forests have a well-developed O horizon with leaf litter thickness measurements of 10 cm or more in the upland forest. Non-native earthworms, which have depleted much of the topsoil regionally, are in low abundance.

The development of the current ecosystems at what is now Seven Lakes has been a dynamic process with many changes in community type since the retreat of the last glaciers around 9,000 years ago. Boreal forest zone conifers such as *Picea* spp., *Larix laricina*, *Pinus banksiana*, and *Abies balsamea* were among the first trees to arrive after the ice sheets melted. *Pinus strobus*, *Acer* spp., *Quercus rubra*, and *Tsuga canadensis* arrived around six to seven thousand years ago, and *Fagus grandifolia* was the last dominant tree species to arrive, approximately 4,000 years ago. The latter species is close to its western range limit. The community composition became relatively stable around 3,000 to 4,000 years ago when the current dominant natural communities were established (Davis 1983).

Over the past few thousand years, the primary community-level altering disturbance forces have been fire and windthrow. Fire has been a community-altering force in the region's low elevation pine-dominated systems, which receive more frequent and extensive burns (Zhang et al. 1999). Red and jack pine-dominated areas within a few tens of kilometers to the east between northern Luce County and Whitefish Point and to the south in Seney National Wildlife Refuge were known to experience large fires (Zhang et al. 1999; Anderson 1982). An analysis of original land survey notes revealed that fire was a rare occurrence in the higher terrain northern hardwood forests of the Luce District, which includes this area with stand-replacing fires only occurring every 2,600 years (Zhang et al. 1999). However, old fire scars were found to be common in several parts of Seven Lakes, and it is suspected to be from the great cutover era in the late 1800s and early 1900s. A nearby post great-cutover fire occurred a few kilometers to the west at the Kingston Plains, which burned everything, including the organic soil. Much of the area is still covered in open stump barrens dominated by lichens, grasses, and bracken fern (Barrett 1997). Most areas with old fire-scarred stumps at Seven Lakes are now under a canopy of maple and beech and are unlikely to burn under current conditions. The abundance of old sawed white pine stumps in the area suggests that white pine was far more common, and perhaps fire did occur here more often in the distant past; but without trees with pyrogenic characteristics such as pines, fire is less likely. This process of mesophication, in which forest structure and leaf litter composition change to make fire less likely, has been documented elsewhere in eastern North America and is related to habitat fragmentation and a shift from the widespread use of fire by indigenous peoples towards a policy of fire suppression (Nowacki and Abrams 2008). Large areas of blowdown from wind events have been observed elsewhere in the region (Woods 2004). We have not seen evidence of such events at Seven Lakes. However, high winds have had some impact, particularly among American beech trees, which had their tops blown off after becoming weakened by beech scale (*Cryptococcus fagisuga*).

MATERIALS AND METHODS

Surveys

Initial survey work began as part of an all-taxon biological inventory in fall 2016 (October 7–10) and continued throughout the 2017 growing season (May 7–11, June 10–13, August 10–13, August 31–September 1, and October 15–16). The initial survey focused on the core area (Seven Lakes Forest Preserve). More intensive surveys started in 2020 and included areas outside the core area and parts of the core area that were not previously surveyed (May 3–4, May 21–24, June 18–21, July 17–20, August 12–16, September 21–25, October 16–19, 2020, and April 30–May 3, May 11–14, June 28–July 5, August 2–8, September 25–28, November 6–8, 2021). Follow-up surveys were conducted in 2022 (June 2–4, August 4–6, October 13–16) and targeted species that were listed from previous surveys, but not documented. The goals of the surveys were to describe the natural communities based on the system developed by the Michigan Natural Features Inventory (Cohen et al. 2015) and to catalog all taxa, including the flora, as completely as possible. Surveys for plants were mostly intuitive meander searches in all habitats present on the property during the appropriate survey periods for all vascular plant taxa. Surveys were primarily conducted by the first author, Ryne Rutherford.

Significant assistance was provided by the second author, Dr. Susan Fawcett, and Dr. Bruce Baldwin during the 2017, 2020, and 2022 seasons. Voucher specimens were collected for new county records and underrepresented taxa. Voucher specimens collected by Ryne Rutherford were deposited at the University of Michigan Herbarium (MICH), and those collected by Susan Fawcett were deposited at the University of Michigan Biological Station Herbarium (UMBS). A project was created in the free global online biodiversity database, iNaturalist, to document the flora with photo vouchers (iNaturalist 2023). The project targets all taxa that could be photographed or identified with microscopy, but the relevant subset can be retrieved by querying 'tracheophyta'.

Floristic Quality Assessment (FQA)

A Floristic Quality Assessment was performed with the Universal FQA Online Calculator (Freyman et al. 2016) using the most recent Michigan database (Reznicek et al. 2014), which assigns each species a coefficient of conservatism (C), a wetness coefficient (W), and categories for physiognomy (e.g., tree, shrub etc.) and duration (e.g., annual, perennial, etc.). Floristic Quality Assessments are increasingly employed by conservationists, land managers, government agencies, and researchers. The Floristic Quality Assessment was developed in the Chicago region (Swink and Wilhelm 1979) as a simple, quantitative, repeatable metric to assess the integrity of remnant native habitats. Within a given region, each species is assigned a coefficient of conservatism (C, or C-value) on a scale of 0 to 10, which corresponds to its tolerance of anthropogenic disturbance (lower coefficients) and/or fidelity to a particular habitat (higher coefficients). For example, all non-native species are automatically assigned a 0, along with some native species that are well-adapted to human disturbance and are without strict habitat requirements (e.g., *Lobelia inflata*), while a species with strict habitat requirements that is intolerant of habitat degradation would be assigned a 10 (e.g., *Kalmia polifolia*) (Reznicek et al. 2014; Slaughter et al. 2015). The Total Mean C is the average of the C-values of all species in the survey, while Native Mean C excludes all non-native species. The Total or Native Floristic Quality Index (FQI) is the Total Mean C, or Native Mean C, respectively, in each case multiplied by the square root of the number of species in the study area—all species for the Native FQI and native species only for the Native FQI. The Adjusted FQI (defined as the Mean C of native plants divided by 10 multiplied by the square-root of the number of native plants divided by the square root of the number of all plants multiplied by 100) was developed to diminish the influence of species richness and to better reflect the impacts of disturbance on species composition (Miller and Wardrop 2006). Coefficients of wetness (W) are widely used for wetland delineation, and species are assigned a number on a five-point scale: Upland (UPL; W= 5); Facultative Upland (FACU; W= 3); Facultative (FAC; W= 0); Facultative Wetland (FACW; W= –3); and Obligate Wetland (OBL; W= –5). Mean Wetness is the average W for all species, and Native Mean Wetness excludes non-native species. The FQI metrics were designed to operate at a variety of scales using various sampling approaches and has been proven to be a robust and forgiving measure of habitat integrity under a variety of conditions (Spyreas 2016, 2019). The Universal FQA Calculator (Freyman et al. 2016) has facilitated this approach by automating calculations and enabling data sharing. This allows for standardized comparisons between sites and the potential to perform large-scale meta-analyses with data from more than 15,000 FQAs now publicly available.

RESULTS

Natural Plant Communities

The descriptions below of the communities found at Seven Lakes include the dominant plant species for both upland and wetland natural communities. The plant communities recognized here follow the Michigan Natural Features Inventory community classification (Cohen et al. 2015). Photos of a selection of natural communities are shown in Figure 2 and selection of vascular plants observed is pictured in Figure 3. A species list is provided in Appendix 1.

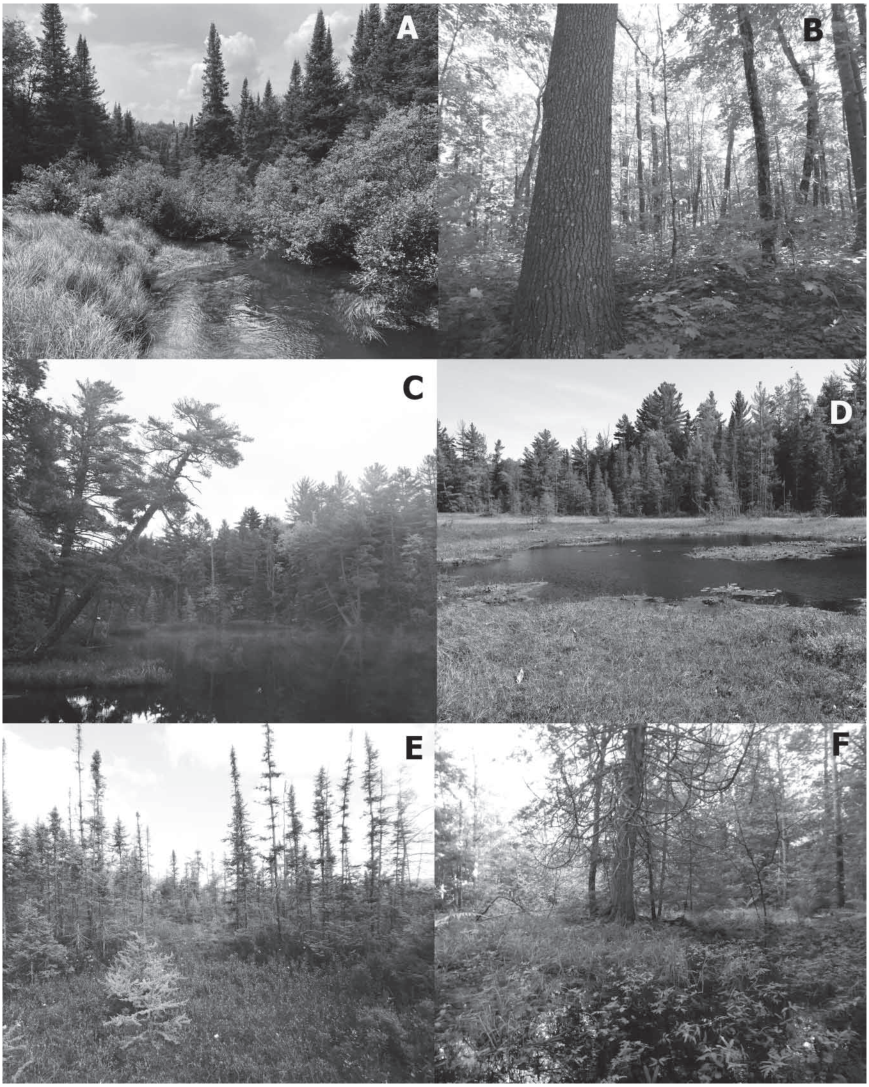

FIGURE 2. Representative habitats of the Seven Lakes Nature Preserve A. Northern shrub thicket along the Fox River. B. Supercanopy white pine in a mesic northern forest. C. Dry-mesic northern forest along the shores of Gopher Lake. D. A pool in an open bog. E. Black spruce and tamarack in a poor conifer swamp. F. Rich conifer swamp with northern white cedar. All photos by R. D. Rutherford.

Forest Group

Forest covers most of Seven Lakes and the rest of the region. It is especially prevalent on the glacial moraines, sandy ridges, and upland areas of the pitted outwash plain. The forest types are strongly tied to the water-holding capacity of the soils and proximity to the water table. American beavers (*Castor canadensis*) have an impact on the forest composition near the water, with deciduous trees felled at higher frequency leading to conifer dominance around waterways. The high snow cover makes this area poor habitat for overwintering deer. Our camera trap study from our all-taxon biodiversity inventory shows that white-tailed deer (*Odocoileus virginianus*) are mostly absent at Seven Lakes between January and March, contributing to minimal observed impacts of browsing. The presence of wolves (*Canis lycaon*) may also prevent large concentrations of yarding deer, lessening impacts on species subject to winter browse.

Mesic Northern Forest

Mesic northern forest is the dominant forest type and has been since the original land surveys in the 1800s (Albert 1995, Zhang et al. 1999). The hilly uplands underlain by coarse-textured glacial till are covered mostly by this forest type, which occurs on over 50% of the land area in the region. This forest type reaches its finest development on the areas of higher terrain with more nutrient-rich fine-textured glacial till. The mesic northern forest in this area has a well-stratified canopy structure. *Acer saccharum* is the dominant tree, with *Betula alleghaniensis* and *Prunus serotina* in lower abundance. Few *Pinus strobus* trees remain in this forest type, but evidence from old stumps suggests it was prevalent prior to historical logging. Relict supercanopy *Pinus strobus* is rare but persists in a few small areas (Figure 2). Although the ground flora is usually more depauperate at Seven Lakes than at Pictured Rocks National Lakeshore to the north and the more calcium-rich mesic northern forests associated with the Niagara Escarpment to the south, some areas of rich ground flora occur on the caps of fine-textured moraines. Species of ground flora characteristic of this forest type include *Streptopus lanceolatus*, *Prunus serotina*, *Lysimachia borealis* (syn. *Trientalis borealis*), *Claytonia caroliniana*, *Erythronium americanum*, *Hepatica americana*, *Carex gracillima*, *C. deweyana*, *C. arctata*, *C. intumescens*, *Maianthemum racemosum*, *Dryopteris intermedia*, *Oxalis acetosella*, *Fallopia cilinodis*, *Aralia nudicaulis*, *Spinulum annotinum*, *Huperzia lucidula*, *Dendrolycopodium dendroideum* and *Polygonatum pubescens*. Areas with sandier soil contain mesic northern forest supporting more *Acer rubrum*, *Fagus grandifolia*, and *Ostrya virginiana*. *Acer pensylvanicum* occurs sporadically here and is near its northwesternmost range limit. *Tsuga canadensis* increases in abundance near lakeshores and streams, particularly on the east and north-facing slopes which have lower evapotranspiration than west and south-facing slopes. Old-growth stands, likely several hundred years old, occur on steep slopes along streams and around lakeshores. It is worth noting that other tree species common in this forest type elsewhere in the Upper Peninsula, such as *Fraxinus* spp., *Tilia americana*, and *Quercus rubra*, were not observed occurring naturally at Seven Lakes, although oaks have been planted on the airstrip.

Dry-Mesic Northern Forest

Dry-mesic northern forest occurs in a few pockets where the soil is slightly poorer and more acidic. Historically abundant in the Upper Peninsula, but now much less common after the great cutover circa 1900, this white pine-dominated forest type occurs along the eastern and northern (west and south-facing) shorelines of several lakes (Figure 2). Only a few hectares of this forest type were found in the study area. *Diervilla lonicera*, *Epigaea repens*, *Gaultheria procumbens*, *Cypripedium acaule*, *Clintonia borealis*, and *Maianthemum canadense* were strongly associated with this forest type.

Dry Northern Forest

Dry northern forest dominated by *Pinus resinosa* is found in small areas of low glacial outwash plain with sandy ridges close to the water table. This open forest type occurs on sandy uplands and is surrounded by poor conifer swamp and bog communities. Although some individuals of *Pinus resinosa* appear to be planted, old stumps suggest some of the area was dominated by that species historically. The few deciduous trees present include *Prunus pensylvanica* and *Acer rubrum*. *Picea glauca* and *Picea mariana* are also present. *Vaccinium angustifolium*, *V. myrtilloides*, *Coptis trifolia*, *Lycopodium clavatum* (Figure 3), and *Gaultheria procumbens* are common in the understory.

Forested and Shrub Wetland Groups

Although forested wetlands cover far less acreage than upland forests, significant areas of these community types are present at Seven Lakes, usually in low-lying areas of sandy pitted outwash plain near rivers and lakes and in isolated kettle depressions where they are associated with open bogs.

Northern Shrub Thicket

Northern shrub thicket occurs abundantly along the floodplains of streams (Figure 2). The short canopy of northern shrub thicket is almost entirely composed of *Alnus incana* and contains nutrient-rich soils shaped by fluctuating water levels and beaver activity. The rich ground flora in the floodplains includes *Calamagrostis canadensis*, *Onoclea sensibilis*, *Rubus strigosus*, *Clematis virginiana*, *Scutellaria galericulata*, *Prunus virginiana*, *Impatiens capensis*, *Thalictrum dasycarpum*, *Osmunda spectabilis*, *Glyceria canadensis*, *Solidago rugosa*, *Viburnum cassinoides*, *Symphyotrichum lateriflorum*, *Ludwigia palustris*, *Caltha palustris* (Figure 3), and *Juncus canadensis*.

Poor Conifer Swamp

Poor conifer swamp is prevalent on acidic peat in association with lake edges and open bog margins. *Picea mariana* and smaller amounts of *Larix laricina* form the canopy, which varies from closed to partially open (Figure 2). *Sphagnum* moss covers the soggy ground from which a variety of shrubs emerge, such as *Rhododendron groenlandicum*, *Viburnum cassinoides*, and *Vaccinium myrtilloides*. The ground flora is similar to that of open bogs and includes *Sarrace-*

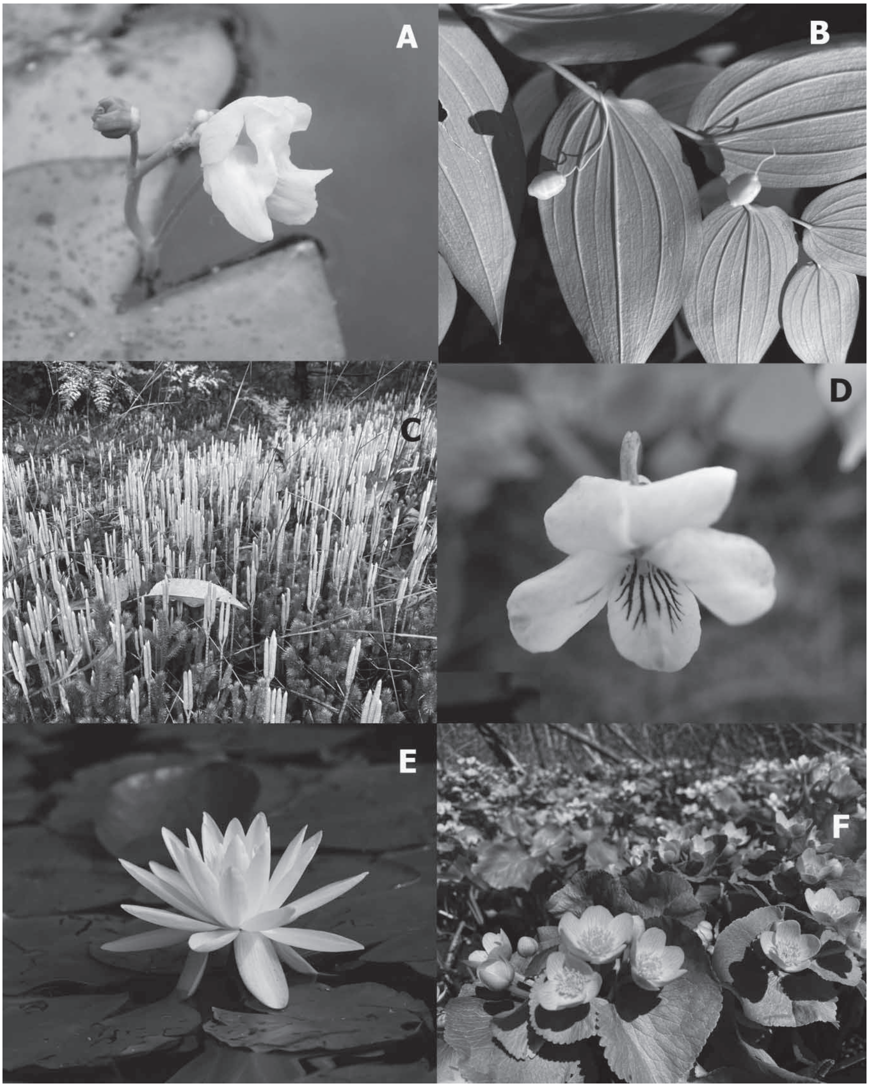

FIGURE 3. Vascular plants of the Seven Lakes Nature Preserve. A. *Utricularia purpurea*. B. *Streptopus amplexifolius*. C. *Lycopodium clavatum*. D. *Viola blanda*. E. *Nymphaea odorata*. F. *Caltha palustris*. All photos by R. D. Rutherford except B. and D by S. Fawcett.

nia purpurea, *Osmundastrum cinnamomeum*, and *Eriophorum vaginatum*. Sedges are abundant in the understory, among which *Carex pauciflora*, *C. limosa*, *C. trisperma*, and *C. buxbaumii* are the most common.

Rich Conifer Swamp

Rich conifer swamp occurs where the water table meets the surface in areas of groundwater flow. This community type is much more nutrient-rich and less acidic than other community types at Seven Lakes. A few stands of sizeable *Thuja occidentalis* remain in narrow bands along spring-fed streams (Figure 2). Common species in this community include *Matteuccia struthiopteris*, *Lysimachia borealis*, *Chrysosplenium americanum*, *Carex canescens*, *C. scabrata*, *Scutellaria galericulata*, *S. lateriflora*, *Mentha canadensis*, and *Streptopus lanceolatus*. One small patch of *Streptopus amplexifolius* (Figure 3) was also discovered.

Open Wetlands—Marsh, Fen, and Bog Groups

Although open wetlands at Seven Lakes generally cover small areas, they host high levels of biodiversity and are home to many specialized wetland species. Hydroperiod, nutrient availability and pH are among the more important factors that dictate the occurrence of these community types.

Northern Wet Meadow

Northern wet meadow often occurs along flowages that were once occupied by standing water resulting from beaver activity. Thick organic soils developed during decades of sediment deposition. A few excellent examples of this community are present at Seven Lakes, where they are dominated by *Carex lasiocarpa*, *Calamagrostis canadensis*, *Solidago canadensis*, *Symphyotrichum lateriflorum*, *Iris versicolor*, *Epilobium leptophyllum*, *Lysimachia terrestris*, *L. thyrsiflora*, *Verbena hastata*, *Spiraea alba*, *Glyceria canadensis*, *Scirpus cyperinus* and *Palustricodon aparinoides* (syn. *Campanula aparinoides*). *Viola blanda* (Figure 3) was often encountered along the upland margins. *Cirsium palustre* is a noteworthy non-native that is common in wet meadows here. Due to the abundant late summer flowers, this plant community is important for pollinators such as bumble bees (*Bombus*) and flower flies (Family Syrphidae). It is presumed that natural succession will eventually shift towards forested wetlands, but the process is slow, and it is likely that these wet meadows will stay open for a long time.

Emergent Marsh

Emergent marsh is a tall, graminoid-dominated aquatic community characterized by vegetation that emerges from the water. Small patches occur along the margins of lakes and stream flowages. Plants common in emergent marsh include *Typha latifolia*, *Schoenoplectus tabernaemontani*, *Carex lasiocarpa*, *Persicaria amphibia*, *Nuphar variegata, Rosa palustris*, and *Myrica gale*. A variation of this community occurs on mucky peat at Moose Lake where the following species occur along with the previous listed species *Eleocharis flavescens*, *E. ovata*, *E. quinqueflora*, *E. palustris*, *Schoenoplectus subterminalis* and *Nymphaea odorata* (Figure 3).

Submergent Marsh

Submergent marsh is well represented at Seven Lakes. This plant community is composed of aquatic plants and forms the structure and base of the aquatic food web that supports waterfowl, aquatic insects, fish, turtles, and amphibians. Most of the lakes sampled are circumneutral to acidic with deep organic muck bottoms. Aquatic plants in the lakes include *Brasenia schreberi*, *Nuphar variegata*, *Nymphaea odorata*, *Najas flexilis*, *Persicaria amphibia*, *Myriophyllum sibiricum*, *M. heterophyllum*, *Elodea canadensis*, *Ceratophyllum demersum*, *Bidens beckii*, *Schoenoplectus tabernaemontani*, *Equisetum fluviatile*, *Potamogeton alpinus*, *P. friesii*, *P. epihydrus*, *P. pusillus*, *P. zosteriformis*, *P. natans*, *P. robbinsii*, and *P. praelongus*, *P. obtusifolius*, and *P. amplifolius*. A freshwater sponge (*Spongilla lacustris*) is found in a few places and is a good indicator of water quality. A different community of submergent plants occurs at Triangle Lake, which is acidic and with a sandy bottom. Rare plants such as *Utricularia purpurea* (Figure 3) and state special concern *Potamogeton confervoides* occur here in abundance. The remoteness of the lakes and lack of public boat access have kept them free of aquatic invasive plants.

Poor Fen

Poor fen is a bog-like community that develops on acidic peat soil with minimal to moderate influence of groundwater. The plant community contains a flora similar to that of bogs, but with the addition of several species that are less tolerant of highly acidic bog conditions. *Arethusa bulbosa*, *Oclemena nemoralis*, *Carex utriculata*, *C. lasiocarpa*, *C. trisperma*, *C. utriculata, C. oligosperma*, *Dulichium arundinaceum*, and *Menyanthes trifoliata* were all noted in this habitat. Examples of this community occur around flowages and outflows of lakes and are often adjacent to other wetland types.

Bog

Bogs are nutrient-poor acidic peatlands that lack influence from groundwater and that are fed mostly from rain and snow. This highly specialized plant community (Figure 2) occurs in scattered, isolated pockets in kettle depressions throughout the area. Many of the lakes in this area are in transition towards becoming bogs. Highly specialized plants such as *Sarracenia purpurea*, *Andromeda glaucophylla*, *Chamaedaphne calyculata*, *Kalmia polifolia*, *Carex pauciflora*, *Carex oligosperma*, *Eriophorum virginicum*, *Vaccinium oxycoccos*, *Rhynchospora alba*, *Xyris montana*, and *Lycopodiella inundata* occur in this community. This is a highly specialized, low pH community containing many species that range further north. Some specialist animals include the bog copper butterfly (*Lycaena epixanthe*), which is common in the kettle bogs at Seven Lakes, and the uncommon and state special concern incurvate emerald dragonfly (*Somatochlora incurvata*). A unique mobile variant of this community that we referred to as "log bogs" occurs on top of old logs in several of the lakes.

Human-modified Communities

Human-modified communities occupy relatively little land area at Seven Lakes but contain species that would likely not occur in the area under natural conditions. The most striking anthropogenic feature is an old airstrip that is in the process of being reforested and contains a mix of native and non-native open country plants. This area was once mesic northern forest but was cleared and leveled to create a private airfield and has suffered from soil compaction and sandy blowouts. Fortunately, much has been done to restore it. The area has been planted with native tree species that include *Acer rubrum*, *Populus tremuloides*, *Pinus strobus*, *P. banksiana*, *P. resinosa*, *Quercus rubra*, and *Quercus macrocarpa*. While the last-named species is not native locally, it may fare well in this location under a warmer climate. Nearly all the trees appear to be doing well, and there have been some signs of natural regeneration. In 2020 and 2021, we observed young jack pine seedlings establishing in open sandy blowout areas, a good sign of recovery. Additional non-native taxa were associated with roadsides, two-tracks, and the periphery of the cabins at the north end of Gopher Lake. A spreading patch of non-native *Betula pendula* occurs around the cabins, but it appears unlikely to succeed in invading the adjacent forest.

Floristic Inventory

Two-hundred ninety-nine species were found on the initial all-taxon biological inventory (Rutherford 2018). That number increased to 462 after surveys in 2020 and 2021 and now stands at 493 and four hybrids after follow-up surveys in 2022. One-hundred forty-seven species are represented by specimen vouchers and 440 are represented by photo vouchers. The richness observed at Seven Lakes includes more than half of the species documented for Alger County (MICHIGAN FLORA ONLINE 2011), which is notable considering that Seven Lakes lacks Great Lakes shoreline and calcareous habitats, which contribute much to the floristic diversity of the region.

The Seven Lakes iNaturalist project (iNaturalist 2023) includes 1048 observations of vascular plants, representing georeferenced observations of 440 species. iNaturalist observations are especially useful for non-destructive documentation of rare and sensitive species (e.g., *Streptopus amplexifolius*) and may complement, but do not replace, herbarium collections. Continuing survey efforts at Seven Lakes will prioritize the collection of voucher specimens.

Forty-six species are provisionally included on the basis of observations alone and are not represented by specimens or photos in the iNaturalist project (indicated with an asterisk in Appendix 1) and are therefore in need of further verification. Many of these were seen during the first years of the study and were not relocated in subsequent years. Taxonomy follows MICHIGAN FLORA ONLINE (2011) with some exceptions, in which case the synonyms used in Michigan Flora are provided in the Appendix.

TABLE 1. Results of the Floristic Quality Assessment, counts of species richness, physiognomy, and duration, and mean coefficients of wetness.

Conservatism-based Metrics		Physiognomy	
Total Mean C	4.5	Tree	32 (6.5%)
Native Mean C	5.3	Shrub	59 (12%)
Total FQI	99.9	Vine	5 (1%)
Native FQI	108.5	Forb	259 (52.5%)
Adjusted FQI	48.9	Grass	34 (6.9%)
% C Value 0	17.6%	Sedge	67 (13.6%)
% C Value 1-3	19.1%	Rush	5 (1%)
% C Value 4-6	39.4%	Ferns/Lycophytes	32 (6.5%)
% C Value 7-10	23.9%		
Native Tree Mean C	4.1		
Native Shrub Mean C	5.3		
Native Herbaceous Mean C	5.4		
Species Richness		**Duration**	
Total Species	493	Annual	37 (7.5%)
Native Species	419 (85%)	Perennial	438 (88.8%)
Non-native Species	74 (15%)	Biennial	18 (3.7%)
Species Wetness		Native Annual	18 (3.7%)
		Native Perennial	393 (79.9%)
Mean Wetness	–0.8	Native Biennial	8 (1.6%)
Native Mean Wetness	–1.6		

Floristic Quality Assessment

Excluding hybrids, 493 species were included in a Floristic Quality Assessment. Of these, 85% are native. The Total Mean C was 4.5, and the Native Mean C was 5.3 (Table 1). The Total FQI was 99.9, and the Native FQI was 108.5. The Total Mean Wetness was –0.8 and Native Mean Wetness was –1.6, reflecting a large proportion of wetland species. Thirty-six percent of species were given a wetness coefficient of –5, indicative of obligate wetland species. The mature forest and wetland ecosystems subject to infrequent disturbance at Seven Lakes are dominated by perennials (88.8% of species). More than half of the species diversity was represented by forbs (52.5%). The summarized results of the Floristic Quality Assessment, including data reflecting physiognomy, growth habit, and mean coefficients of wetness are presented in Table 1, and the complete dataset, downloadable in spreadsheet form, is available online (Universal FQA Calculator 2023).

County Records

Sixteen species representing new county records for Alger County were vouchered and verified. These are *Acer platanoides*, *Anemone quinquefolia*, *Betula pendula, Epipactis helleborine, Erucastrum gallicum*, *Galium trifidum*, *Hemerocallis fulva, Hydrocotyle americana*, *Hylotelephium telephium, Leersia oryzoides*, *Malus domestica, Muscari botryoides*, *Pinus sylvestris*, *Potamogeton* *pusillus*, *Rhinanthus minor,* and *Thelypteris palustris*. No new county records were collected from Schoolcraft County.

DISCUSSION

Like other floras in the northern Great Lakes/Laurentian latitudinal belt, the plants at Seven Lakes are a mix of the eastern deciduous floristic province to the south and the boreal forest to the north. Much of the flora here ranges eastward to the Atlantic coast and south along the Appalachian chain. Some species with that distribution pattern reach their western range limit in the central Upper Peninsula (e.g., *Acer pensylvanicum*, *Fagus grandifolia*, *Medeola virginiana*). A species of poor fens and bogs, *Oclemena nemoralis*, is also predominantly northeastern in distribution and is near its western range limit.

A few other species are predominantly western in distribution and are disjunct in the Laurentian-Great Lakes region (e.g., *Streptopus amplexifolius*, *Erythranthe geyeri*, *Polygonum douglasii*, *Vaccinium membranaceum*, *V. ovalifolium*, *Goodyera oblongifolia*, *and Osmorhiza berteroi*) (Marquis and Voss 1981). Many more western disjuncts are present at Pictured Rocks National Lakeshore, the Keweenaw Peninsula and the western Upper Peninsula (Read 1975). At Seven Lakes, regionally rare western bilberries (*Vaccinium membranaceum* and *V. ovalifolium*) occur in abundance under a canopy of mature eastern hemlock resulting in a distinct botanical association that occurs only in the vicinity of Pictured Rocks National Lakeshore. Although many wide-ranging boreal plants are common at Seven Lakes, few are rare regionally, with *Amelanchier bartramiana* representing such an exception.

Several southern species strongly associated with mesic northern forest such as *Fraxinus* spp., *Tilia americana*, *Ostrya virginiana*, and *Quercus* spp., *Trillium grandiflorum*, *Sanguinaria canadensis*, and *Caulophyllum thalictroides* do not occur naturally at Seven Lakes. These species are all common in deciduous forests associated with the calcareous formations to the south near the Niagara Escarpment and on top of cliffs at Pictured Rocks National Lakeshore, which is capped with calcareous rock, resulting in a rich flora (Read 1975). The deciduous forests at Seven Lakes seem to be calcium limited, leading to lower floristic diversity.

Only one state-listed species, *Potamogeton confervoides*, was detected at Seven Lakes. An abundance of state-listed and a few federally-listed species are present in the region, but the habitats that support those rare species (e.g., Great Lakes dunes, coastal alvars, Niagara Escarpment) are not present at Seven Lakes.

In the Floristic Quality Assessment, species with a C-value > 7 are considered to occur under conditions similar to those under which they evolved, and make up 19% of the surveyed species, while those with C-values < 3 include natives and non-natives tolerant of anthropogenic disturbance, and constitute about 27% of total species (Freyman et al. 2016). The FQI does not incorporate relative abundance of constituent species, and most non-native species as well as native species with low C-values were in low abundance, and largely restricted to disturbed areas. A majority of non-native species in the region are dependent on anthropogenic disturbance, and, with few exceptions (discussed below), fail to establish beyond a few meters from roadsides or other human structures and clearings, a pattern described more than a hundred years ago in northern lower Michigan (Gleason and MacFarland 1914; Gleason 1918), and consistent with our findings at this site. According to Herman et al. 2001, for Michigan, an area with an FQI of 35 or greater is considered floristically important, and sites with an FQI of 50 or greater are of exceptional value for the conservation of Michigan's biodiversity, although these scores may be impacted by parcel size and habitat type (Slaughter et al. 2015). The Total FQI of 99.9 for Seven Lakes reflects its high integrity and limited history of anthropogenic disturbance, but should be interpreted with consideration of the large geographic extent of the parcel and the pooled data from a diversity of plant communities.

Non-native Species

Although several non-native species were found, only one, *Centaurea stoebe*, is included on the list of invasive species maintained by the State of Michigan (Michigan Invasive Species Program 2023). This species is widespread throughout the Great Lakes region and is documented from all counties in the Upper Peninsula. The J.A. Woollam Foundation has already made significant progress towards eradication of this species on the property. Most of the remaining non-native species are characteristic of disturbed habitats and were found in low abundance, mostly on the sandy airstrip, along roadsides, or in the vicinity of cabins. The limited number of roads in and around the Seven Lakes, the low-nutrient soils, and the cessation of broad-scale timber extraction have greatly limited opportunities for the incursion of weeds. Despite the low level of overall impact, a high proportion of the new county records were non-natives. Several were likely overlooked in previous collection efforts, but some may have arrived recently. Nearly all of them were collected from roadside patches and do not currently represent a threat to the ecosystems at Seven Lakes. These species include *Acer platanoides*, *Betula pendula, Epipactus helleborine, Erucastrum gallicum*, *Hemerocallis fulva, Hylotelephium telephium, Malus domestica, Muscari botryoides*, *Pinus sylvestris*, and *Rhinanthus minor*.

A notable invader is *Cirsium palustre*, which has successfully colonized the largely intact interior wetlands, especially wet meadows, and some conifer swamps where it thrives and may potentially compete with native species. Another invader, *Lapsana communis*, was listed as rare in the initial survey of Pictured Rocks National Lakeshore (Read 1975) but is now common along tracks and trails in mesic northern forest throughout the Upper Peninsula, including at Seven Lakes. The upland forests are generally free of invaders, although *Epipactis helleborine* was occasionally seen in minimally-disturbed upland forests.

Future Threats

The potential arrival of the hemlock woolly adelgid (*Adelges tsugae*) is concerning under future climate change scenarios (Ellison et al. 2018). Early assessments suggested that the northwesternmost populations of eastern hemlock found in the Lake Superior basin occur in an area that is too cold for the hemlock woolly adelgid, but recent climate change models show that this might not be true in the coming decades. At the time of this writing, it had recently been found in northwestern lower Michigan, about 250 kilometers to the south. At Seven Lakes, eastern hemlock is typically found within a few tens of meters of streams, lakes, and bogs but is infrequent in uplands. Perhaps the sandy soils limit it from becoming a co-dominant upland tree.

The sandy soils may be a factor in climate change scenarios for other species as well. While the moist regional climate allows for the development of mesophytic forest on potentially drought-prone sites, water stress will likely increase in the future, possibly altering the current species assemblage. During warmer and drier periods post glaciation, red oak, red maple, and white pine forest occurred where northern hardwood forest now dominates at the Sylvania Wilderness Area in the western Upper Peninsula (Davis et al. 1998). It is quite plausible that the current assemblage of sugar maple, American beech, yellow birch, eastern hemlock, and black cherry might shift to a more drought-tolerant forest type with a greater abundance of red oak, red maple, and white pine. However, the hilly topography and abundance of wetland and water interface will likely provide refuge for more moisture-loving trees in the future (McLaughlin et al. 2017).

It is unclear how the wetlands will be impacted by climate change. While some climate change-related impacts are expected, it is worth noting the resilience of peatlands to changing climates in the region. Sphagnum bogs with flora like those in the Upper Peninsula occur as far south as northern Indiana, where they are considered glacial relicts (Wilcox and Simonin 1988).

Despite the threats from climate change, local anthropogenic impacts will likely be minimized, given the shift toward full protection of much of this area. Large blocks of continuous natural cover make it more feasible for species to shift their distributions in response to changing physical and biological conditions. Beyond the boundaries of Seven Lakes, little mature forest remains, and a more aggressive timber management cycle persists, thereby increasing the regional importance of the older intact natural communities at Seven Lakes. The abundance of intact forests, lakes, wetlands, and stream corridors and the lack of roads mean that broad-scale ecosystem processes will likely continue far into the future.

CONCLUSION

In an era of accelerating climate change and biodiversity loss, it can be challenging to determine how best to prioritize limited resources for maximum conservation benefit. While we recognize the benefits of targeting small, fragmented areas, especially for the conservation of rare species (Wintle et al. 2019) or the stewardship of natural areas near urban centers (Schwartz 2006), we applaud the vision of the J.A. Woollam Foundation in consolidating and protecting large tracts of highly intact natural communities. These habitats are irreplaceable, and the most successful restoration effort is never a substitute for preserving preexisting wildlands. We believe that the acquisition and preservation of intact natural communities, especially in areas where land is still relatively undeveloped and affordable, is a highly impactful and cost-effective use of conservation funds. It is our sincerest hope that more organizations will follow suit. This place at the headwaters of the Fox River and the undisputed solitude it provides was immortalized by Ernest Hemingway's short story, "Big Two-Hearted River" (Gibbs 1983), and that timeless wildness is still reported by all who visit. Long may it be that way.

AUTHOR CONTRIBUTIONS

RR and SF conceived this study, created the study design, and collected the specimens. RR drafted the manuscript. RR and SF edited, and revised the manuscript. SF designed the figures and conducted the analyses.

ACKNOWLEDGMENTS

Many thanks to Cathy Rustermier, Amanda Greenburg, and John A. Woollam at the J.A. Woollam Foundation for financial support of this inventory work and for providing on-site lodging. We thank Bruce Baldwin for his assistance with botanical surveys. We thank Michael Huft for his significant edits which helped improve the quality of this article greatly. We thank Dan Skean and an anonymous reviewer for helpful edits of the manuscript. We thank A. A. Reznicek (MICH) for assistance with determinations and the University of Michigan Biological Station (UMBS) for research support. We are grateful to the members of the iNaturalist community who contributed observations and helped with identifications, especially Bob Kahl, Rob Routledge, Alex Graeff and Étienne Lacroix-Carignan. Thanks to Andrew Burton for reviewing early drafts of this manuscript. Thanks to Tina Hall for facilitating our partnership with the J.A. Woollam Foundation and to David Boehlke for providing the GIS layers for the map. We thank caretaker John Herman for stewardship of the Seven Lakes Preserve and for facilitating our research and the Nature Conservancy for helping with the acquisition, study, and conservation of this land.

LITERATURE CITED

Albert, D. A. (1995). Regional landscape ecosystems of Michigan, Minnesota, and Wisconsin: a working map and classification. General Technical Report NC-178. St. Paul, Minnesota: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station. Northern Prairie Wildlife Research Center Home Page, Version 03JUN98. Available at: http://www.npwrc.usgs.gov/resource/1998/rlandscp/rlandscp.htm (Accessed March 28, 2023).

Anderson, S. H. (1982). Effects of the 1976 Seney National Wildlife Refuge wildfire on wildlife and wildlife habitats. U.S. Fish Wildlife Services Resources Publication No. 146.

Barrett, L. R. (1997). Podzolization under forest and stump prairie vegetation in northern Michigan. Geoderma 78: 37–58.

Cohen, J. G., M. A. Kost, B. S. Slaughter, and D. A. Albert. (2015). A field guide to the natural communities of Michigan. Michigan State University Press, East Lansing.

Davis, M. B. (1983). Holocene vegetational history of the eastern United States. Pp. 166–181 in Late-Quaternary environments of the United States. Volume II: The Holocene. H. E. Wright, editor, University of Minnesota Press, Minneapolis.

Davis, M. B., R. Calcotte, S. Sugita, and H. Takahara. (1998). Patchy invasion and the origin of a hemlock-hardwoods forest mosaic. Ecology 79: 2641–2659.

Ellison, A., D. A. Orwig, M. Fitzpatrick, and E. L. Preisser. (2018). The past, present, and future of the hemlock woolly adelgid (*Adelges tsugae*) and its ecological interactions with eastern hemlock (*Tsuga canadensis*) forests. Insects 9 (4), 172. Available at https://doi.org/10.3390/insects9040172 (Accessed March 28, 2023).

Freyman, W. A., L. A. Masters, and S. Packard. (2016). The universal floristic quality assessment (FQA) calculator: An online tool for ecological assessment and monitoring. Methods in Ecology and Evolution 7: 380–383.

Gibb, R. (1983). "He made him up: 'Big Two-Hearted River' as doppelganger." Pp. 254–259 in Critical Essays on Hemingway's 'In Our Time.' M. S. Reynolds, editor. G. K. Hall, Boston.

Gleason, H. A. (1918). The local distribution of introduced species near Douglas Lake, Michigan. Torreya 18: 81–89.

Gleason, H. A., and F. T. McFarland. (1914). The introduced vegetation in the vicinity of Douglas Lake, Michigan. Bulletin of the Torrey Botanical Club 41: 511–521.

Herman, K. D., L. A. Masters, M. R. Penskar, A. A. Reznicek, G. S. Wilhelm, W. W. Brodovich, and K. P. Gardiner. (2001). Floristic Quality Assessment with wetland categories and examples of computer applications for the State of Michigan, Revised, 2nd Edition. Michigan Department of Natural Resources, Wildlife, Natural Heritage Program, Lansing.

iNaturalist (2023). Seven Lakes project available at http://inaturalist.org/projects/seven-lakes. (Accessed March 28, 2023).

Kottek, M., J. Grieser, C. Beck, B. Rudolf, and F. Rubel. (2006). World map of the Köppen-Geiger climate classification updated. Meteorologische Zeitschrift 15: 259–263.

LaBerge, G. L. (1994). Geology of the Lake Superior region. Penokean Press, Oshkosh, Wisconsin.

Marquis, R. J., and E. G. Voss. (1981). Distributions of some western North American plants disjunct in the Great Lakes region. The Michigan Botanist 20: 53–82.

McLaughlin, B. C., D. D. Ackerly, P. Z. Klos, J. Natali, T. E. Dawson, and S. E. Thompson. (2017). Hydrologic refugia, plants, and climate change. Global Change Biology 23: 2941–2961.

MICHIGAN FLORA ONLINE. (2011). A. A. Reznicek, E. G. Voss, and B. S. Walters. University of Michigan. Available at michiganflora.net. (Accessed March 28, 2023).

Michigan Invasive Species Program. (2021). Available at michigan.gov/invasives (Accessed October 10, 2021).

Miller, S.J. and D.H. Wardrop. (2006). Adapting the floristic quality assessment index to indicate anthropogenic disturbance in central Pennsylvania wetlands. Ecological Indicators 6: 313–326.

MRCC. (2021). Climate summary for USC00205690-Munising, Michigan. Available at https://mrcc.purdue.edu/mw_climate/climateSummaries/climSummOut_temp?stnld=USC00205690 Accessed February 11, 2024).

Nowacki, G. J., and M. D. Abrams. (2008). The demise of fire and "mesophication" of forests in the eastern United States. Bioscience 58: 123–138.

Read, R. H. (1975). Vascular plants of Pictured Rocks National Lakeshore, Alger County, Michigan. The Michigan Botanist 14: 3-43.

Reznicek, A. A., M. R. Penskar, B. S. Walters, and B. S. Slaughter. (2014). Michigan floristic quality assessment database. Herbarium, University of Michigan. Ann Arbor, Michigan and Michigan Natural Features Inventory, Michigan State University, Lansing, Michigan.

Rutherford, R. D. (2018). A biological inventory of Seven Lakes Nature Preserve, Alger County, Michigan. J.A. Woollam Foundation. Technical Report. Available online at https://www.researchgate.net/publication/348927077_A_Biological_Inventory_of_Seven_Lakes_Nature_Preserve_Alger_County_MI.

Schwartz, M. W. (2006). How conservation scientists can help develop social capital for biodiversity. Conservation Biology 20: 1550–1552.

Slaughter, B. S., A. A. Reznicek, M. R. Penskar, and B. S. Walters. (2015). Notes on the third edition of the Floristic Quality Assessment of Michigan. Wetland Science and Practice 28–32.

Spyreas, G. (2016). Scale and sampling effects on floristic quality. PloS One, 11(8): e0160693.

Spyreas, G. (2019). Floristic Quality Assessment: a critique, a defense, and a primer. Ecosphere 10(8): e02825.

Swink, F., and G. S. Wilhelm. (1979). Plants of the Chicago region revised and expanded edition with keys. The Morton Arboretum, Lisle, Illinois.

Universal FQA Calculator (2023). Inventory of Seven Lakes. Available at http://universalfqa.org/view_inventory/23442 (Accessed March 17, 2023).

Wilcox, D. A., and H. A. Simonin. (1988). The stratigraphy and development of a floating peatland, Pinhook Bog, Indiana. Wetlands 8: 75–91.

Wintle, B. A., H. Kujala, A. Whitehead, A. Cameron, S. Veloz, A. Kukkala, A. Moilanen et al. (2019). Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity. Proceedings of the National Academy of Sciences116: 909–914.

Woods, K. D. (2004). Intermediate disturbance in a late-successional hemlock northern hardwood forest. Journal of Ecology 92: 464–476.

Zhang, Q. F., K. S. Pregitzer, and D. D. Reed. (1999). Catastrophic disturbance in the presettlement forests of the Upper Peninsula of Michigan. Canadian Journal of Forest Research 29: 106–114.

APPENDIX 1. Checklist of the flora of the Seven Lakes Nature Preserve. Collections numbers of voucher specimens are in brackets; RDR is Ryne D. Rutherford (specimens deposited at MICH) and SF is Susan Fawcett (specimens deposited at UMBS). An asterisk (*) denotes species not represented by voucher specimens or iNaturalist observations. All voucher specimens are from Alger County except RDR 143–146, which were collected from Schoolcraft County. Nomenclature follows MICHIGAN FLORA ONLINE (2023), with some exceptions, in which case the synonyms used in the Michigan Flora are included in parentheses.

LYCOPHYTES

ISOETACEAE

Isoetes echinospora Durieu

LYCOPODIACEAE

Dendrolycopodium dendroideum (Michx.) A. Haines
Dendrolycopodium obscurum (L.) A. Haines [*RDR172*]
Diphasiastrum complanatum (L.) Holub
Diphasiastrum tristachyum (Pursh) Holub [*SF1407*]
Huperzia lucidula (Michx.) Rothm.
Lycopodiella inundata (L.) Holub
Lycopodium clavatum L. [*SF1408*]
Spinulum annotinum (L.) A. Haines

FERNS

ATHYRIACEAE

Athyrium angustum (Willd.) C. Presl (=*Athyrium filix-femina* (L.) Roth) [*SF1362*]

CYSTOPTERIDACEAE

Cystopteris fragilis (L.) Bernh.*
Gymnocarpium dryopteris (L.) Newman

DENNSTAEDTIACEAE

Pteridium aquilinum (L.) Kuhn [*RDR184*]

DRYOPTERIDACEAE

Dryopteris carthusiana (Vill.) H.P. Fuchs [*RDR144*; *RDR275*]
Dryopteris cristata (L.) A. Gray
Dryopteris intermedia (Muhl. ex Willd.) A. Gray [*RDR187*]
Dryopteris ×boottii Underw.

EQUISETACEAE

Equisetum arvense L.

Equisetum fluviatile L.
Equisetum pratense Ehrh.*
Equisetum sylvaticum L. [*RDR274*]
Equisetum variegatum Schleich. ex F. Weber & D. Mohr

ONOCLEACEAE
Matteuccia struthiopteris (L.) Tod.
Onoclea sensibilis L.

OPHIOGLOSSACEAE
Botrychium matricariifolium (Retz.) A.Braun ex W.D.J.Koch
Botrypus virginianus (L.) Michx.
Sceptridium multifidum (S.G. Gmel.) Rupr. [*RDR288*]

OSMUNDACEAE
Osmunda claytoniana L.
Osmunda spectabilis Willd. (=*Osmunda regalis* L.)
Osmundastrum cinnamomeum (L.) C. Presl

POLYPODIACEAE
Polypodium virginianum L.

THELYPTERIDACEAE
Phegopteris connectilis (Michx.) Watt [*SF1933A*]
Thelypteris palustris Schott [*RDR264*; *SF1924*]

GYMNOSPERMS

CUPRESSACEAE
Thuja occidentalis L.

PINACEAE
Abies balsamea (L.) Mill. [*RDR177*]
Larix laricina (Du Roi) K. Koch [*RDR167*]
Picea glauca (Moench) Voss [*RDR178*]
Picea mariana (Mill.) Britton, Sterns & Poggenb. [*RDR164*]
Pinus banksiana Lamb. [*RDR277*]
Pinus resinosa Aiton
Pinus strobus L. [*RDR182*]
Pinus sylvestris L. [*RDR306*]
Tsuga canadensis (L.) Carrière [*RDR196*]

TAXACEAE
Taxus canadensis Marshall [*RDR165*]

ANGIOSPERMS

ALISMATACEAE
Sagittaria latifolia Willd.

AMARANTHACEAE
Chenopodium album L.

AMARYLLIDACEAE
Narcissus sp. L. [*RDR228*]

ANACARDIACEAE
Toxicodendron rydbergii (Small ex Rydb.) Greene

APIACEAE
Cicuta bulbifera L.
Daucus carota L.
Heracleum maximum W. Bartram
Osmorhiza berteroi DC.*
Pastinaca sativa L.

APOCYNACEAE
Apocynum androsaemifolium L.
Asclepias incarnata L. [RDR276]
Asclepias syriaca L.
Vinca minor L. [*RDR170*]

AQUIFOLIACEAE
Ilex mucronata (L.) M. Powell, Savol. & S. Andrews
Ilex verticillata (L.) A. Gray [*RDR173*]

ARACEAE
Arisaema triphyllum (L.) Schott*
Calla palustris L.
Lemna minor L.
Lemna trisulca L.
Spirodela polyrhiza (L.) Schleid.

ARALIACEAE
Aralia hispida Vent.
Aralia nudicaulis L.
Hydrocotyle americana L. [*RDR110*]

ASPARAGACEAE (=CONVALLARIACEAE pro parte)
Muscari botryoides (L.) Mill [*RDR229*]
Maianthemum canadense Desf.
Maianthemum racemosum (L.) Link
Maianthemum trifolium (L.) Sloboda
Polygonatum pubescens (Willd.) Pursh
Hemerocallis fulva (L.) L. [*RDR260*]

ASTERACEAE
Achillea millefolium L.
Anaphalis margaritacea (L.) Benth. & Hook. f. [*RDR146*]
Antennaria howellii Greene*
Arctium minus (Hill) Bernh.
Bidens beckii Torr. ex Spreng. [*RDR246*]
Bidens cernua L.
Centaurea stoebe L. [*RDR183*; *RDR272*]
Cirsium arvense (L.) Scop.
Cirsium palustre (L.) Scop.
Cirsium vulgare (Savi) Ten.
Doellingeria umbellata (Mill.) Nees
Erigeron annuus (L.) Pers.
Erigeron canadensis L. (=*Conyza canadensis* (L.) Cronq.) [*RDR267*]
Erigeron strigosus Muhl. ex Willd.
Eupatorium perfoliatum L.
Euthamia caroliniana (L.) Greene ex Porter & Britton [*RDR133*]

Euthamia graminifolia (L.) Nutt.
Eutrochium maculatum (L.) E.E. Lamont
Hieracium aurantiacum L.
Hieracium kalmii L.
Hieracium piloselloides Vill.
Hieracium scabrum Michx.
Hypochaeris radicata L.
Lactuca biennis (Moench) Fernald
Lactuca canadensis L.
Lapsana communis L.
Leucanthemum vulgare Lam.
Oclemena nemoralis (Aiton) Greene
Pseudognaphalium macounii (Greene) Kartesz [*RDR149*; *RDR262; RDR266*]
Pseudognaphalium obtusifolium (L.) Hillard & B.L. Burtt [*SF1933*]
Solidago altissima L. [*RDR281*]
Solidago canadensis L. [*RDR175*]
Solidago hispida Muhl. ex Willd. [*RDR273*]
Solidago juncea Aiton
Solidago rugosa Mill.
Solidago uliginosa Nutt.
Sonchus arvensis L.
Sonchus asper (L.) Hill
Symphyotrichum boreale (Torr. & A. Gray) Á. Löve & D. Löve [*RDR247*]
Symphyotrichum ciliolatum (Lindl.) Á. Löve & D. Löve
Symphyotrichum lanceolatum (Willd.) G.L. Nesom [*SF1410*]
Symphyotrichum lateriflorum (L.) Á. Löve & D. Löve*
Symphyotrichum puniceum (L.) Á. Löve & D. Löve
Tanacetum vulgare L.
Taraxacum officinale F.H. Wigg.

BALSAMINACEAE
Impatiens capensis Meerb.

BETULACEAE
Alnus incana (L.) Moench [*RDR166*]
Betula alleghaniensis Britton [*RDR162*]
Betula papyrifera Marshall
Betula pendula Roth [*RDR154*]
Betula pumila L.
Corylus cornuta Marshall [*RDR270*]

BORAGINACEAE
Myosotis sylvatica Ehrh. ex Hoffm.

BRASSICACEAE
Barbarea vulgaris W.T. Aiton
Capsella bursa-pastoris (L.) Medik.*
Cardamine pensylvanica Muhl. ex Willd. [*RDR245*]
Erucastrum gallicum (Willd.) O.E. Schulz [*RDR127*]
Lepidium campestre (L.) W.T. Aiton
Nasturtium officinale R.Br.
Rorippa palustris (L.) Besser [*RDR 126*]

CABOMBACEAE
Brasenia schreberi J.F. Gmel. [*RDR299*]

CAMPANULACEAE

Palustricodon aparinoides (Pursh) Morin (=*Campanula aparinoides* Pursh) [*RDR259*]
Lobelia inflata L. [*RDR280*]

DIERVILLACEAE
Diervilla lonicera Mill.

CAPRIFOLIACEAE
Lonicera canadensis Bartram & W. Bartram ex Marshall [*RDR296*]
Lonicera villosa (Michx.) Schult.

CARYOPHYLLACEAE
Cerastium fontanum Baumg. [*RDR294*]
Dianthus armeria L.
Saponaria officinalis L.
Silene latifolia Poir.
Silene vulgaris (Moench) Garcke
Spergularia rubra (L.) J. Presl & C. Presl
Stellaria borealis Bigelow
Stellaria media (L.) Vill.*

CERATOPHYLLACEAE
Ceratophyllum demersum L.

CORNACEAE
Cornus alternifolia L.*
Cornus canadensis L. [*RDR169*]
Cornus sericea L. [*RDR268*]

CRASSULACEAE
Hylotelephium telephium (L.) H.Ohba [*RDR230*]

CYPERACEAE
Carex arctata Boott
Carex bebbii (Olney ex L.H. Bailey) Olney ex Fernald
Carex brunnescens (Pers.) Poir. [*SF1922*]
Carex buxbaumii Wahlenb. [*RDR238*; *SF1930*]
Carex canescens L.
Carex communis L.H. Bailey
Carex comosa Boott
Carex crawfordii Fernald [*RDR150*; *RDR243*; *SF1920*]
Carex crinita Lam.
Carex cryptolepis Mack.
Carex debilis Michx.
Carex deweyana Schwein.
Carex diandra Schrank*
Carex disperma Dewey
Carex echinata Murray
Carex flava L.
Carex gracillima Schwein.
Carex gynandra Schwein.
Carex interior L.H. Bailey
Carex intumescens Rudge [*RDR271*]
Carex lacustris Willd.
Carex lasiocarpa Ehrh.
Carex leptalea Wahlenb.
Carex leptonervia (Fernald) Fernald [*RDR234*]
Carex limosa L.

Carex magellanica Lam.*
Carex michauxiana Boeckeler
Carex oligosperma Michx. [*RDR140*]
Carex pallescens L.
Carex pauciflora Lightf.
Carex peckii Howe
Carex pellita Muhl. ex Willd.
Carex projecta Mack.
Carex pseudocyperus L. [*SF1926*]
Carex retrorsa Schwein.
Carex rostrata Stokes [*SF1925*]
Carex scabrata Schwein. [*SF1363*]
Carex scoparia Schkuhr ex Willd.
Carex sterilis Willd. [*SF1921*]
Carex stipata Muhl. ex Willd.
Carex stricta Lam. [*RDR237*]
Carex tenera Dewey*
Carex tribuloides Wahlenb.
Carex trisperma Dewey [*RDR130*]
Carex utriculata Boott
Cladium mariscoides (Muhl.) Torr.
Dulichium arundinaceum (L.) Britton [*RDR134*]
Eleocharis erythropoda Steud.
Eleocharis flavescens var. olivacea (Poir.) Urb. [*RDR240*; *SF1927*]
Eleocharis intermedia Schult.
Eleocharis ovata (Roth) Roem. & Schult. [*RDR256*]
Eleocharis palustris (L.) Roem. & Schult. [*SF1928*]
Eleocharis quinqueflora (Hartmann) O.Schwarz [*RDR241*; *SF1929*]
Eriophorum angustifolium Honck.
Eriophorum tenellum Nutt.*
Eriophorum vaginatum L.
Eriophorum virginicum L. [*SF1932A*]
Rhynchospora alba (L.) Vahl
Rhynchospora capitellata (Michx.) Vahl
Schoenoplectus acutus (Muhl. ex Bigelow) Á. Löve & D. Löve
Schoenoplectus subterminalis (Torr.) Soják
Schoenoplectus tabernaemontani (C.C. Gmel.) Palla
Scirpus atrocinctus Fernald
Scirpus atrovirens Willd.
Scirpus cyperinus (L.) Kunth
Trichophorum alpinum (L.) Pers.
Trichophorum cespitosum (L.) Hartm.

DROSERAEAE
Drosera intermedia Hayne
Drosera rotundifolia L.

ERICACEAE
Andromeda polifolia L. (=*Andromeda glaucophylla* Link)
Chamaedaphne calyculata (L.) Moench [*RDR141*]
Chimaphila umbellata (L.) W.P.C. Barton
Epigaea repens L. [*RDR190*; *RDR301*]
Gaultheria hispidula (L.) Muhl. ex Bigelow [*RDR168*; *RDR300*]
Gaultheria procumbens L. [*RDR194*]
Gaylussacia baccata (Wangenh.) K. Koch
Kalmia polifolia Wangenh.
Moneses uniflora (L.) A. Gray

Monotropa uniflora L.
Orthilia secunda (L.) House
Pyrola chlorantha Sw.
Pyrola elliptica Nutt.
Rhododendron groenlandicum (Oeder) Kron & Judd [*RDR186*]
Vaccinium angustifolium Aiton [*RDR189*]
Vaccinium macrocarpon Aiton [*RDR139*]
Vaccinium membranaceum Douglas ex Torr.
Vaccinium myrtilloides Michx. [*RDR289*]
Vaccinium ovalifolium Sm. [*RDR188*]
Vaccinium oxycoccos L.

ERIOCAULACEAE
Eriocaulon aquaticum (Hill) Druce

FABACEAE
Lathyrus sp. [*RDR227*]
Lotus corniculatus L.
Medicago lupulina L. [*RDR152*]
Medicago sativa L.
Melilotus albus Medik.
Trifolium aureum Pollich
Trifolium hybridum L.*
Trifolium pratense L.
Trifolium repens L.
Vicia americana Muhl. ex Willd.
Vicia villosa Roth*

FAGACEAE
Fagus grandifolia Ehrh. [*RDR192*]
Quercus macrocarpa Michx.
Quercus rubra L.

GROSSULARIACEAE
Ribes cynosbati L.*
Ribes glandulosum Grauer [*RDR145*; *RDR290*]
Ribes triste Pall.

HALORAGACEAE
Myriophyllum heterophyllum Michx.*
Myriophyllum sibiricum Kom.

HYDROCHARITACEAE
Elodea canadensis Michx.
Najas flexilis (Willd.) Rostk. & W.L.E. Schmidt
Vallisneria americana Michx.*

HYPERICACEAE
Hypericum boreale (Britton) E.P. Bicknell [*RDR137*]
Hypericum canadense L.
Hypericum ellipticum Hook.
Hypericum perforatum L. [*RDR191*]
Triadenum fraseri (Spach) Gleason

IRIDACEAE
Iris versicolor L. [*RDR235*]

JUNCACEAE
- *Juncus articulatus* L.
- *Juncus balticus* Willd.
- *Juncus canadensis* J. Gay ex Laharpe
- *Juncus effusus* L.
- *Juncus tenuis* Willd. [*RDR292*]

LAMIACEAE
- *Clinopodium vulgare* L. [*RDR293*]
- *Galeopsis tetrahit* L.
- *Lycopus americanus* Muhl. ex W.P.C. Barton*
- *Lycopus uniflorus* Michx.
- *Mentha canadensis* L.
- *Prunella vulgaris* L. [*RDR282*]
- *Scutellaria galericulata* L.
- *Scutellaria lateriflora* L.
- *Stachys pilosa* Nutt.*

LENTIBULARIACEAE
- *Utricularia cornuta* Michx.
- *Utricularia intermedia* Hayne
- *Utricularia macrorhiza* Leconte (=*Utricularia vulgaris* L.)
- *Utricularia purpurea* Walter [*RDR298*]
- *Utricularia resupinata* B.D. Greene ex Bigelow

LILIACEAE (=CONVALLARIACEAE pro parte)
- *Clintonia borealis* (Aiton) Raf.
- *Erythronium americanum* Ker Gawl.
- *Medeola virginiana* L.
- *Streptopus amplexifolius* (L.) DC.
- *Streptopus lanceolatus* (Aiton) Reveal

LINDERNIACEAE
- *Lindernia dubia* (L.) Pennell

LINNAEACEAE
- *Linnaea borealis* L.*

MELANTHIACEAE (=TRILLIACEAE)
- *Trillium cernuum* L.

MENYANTHACEAE
- *Menyanthes trifoliata* L.

MOLLUGINACEAE
- *Mollugo verticillata* L.

MONTIACEAE
- *Claytonia caroliniana* Michx.

MYRICACEAE
- *Comptonia peregrina* (L.) Coult [*RDR278*]
- *Myrica gale* L. [*RDR138*]

NYMPHAEACEAE
- *Nuphar variegata* Durand
- *Nymphaea odorata* Aiton [*RDR239*]

ONAGRACEAE
Chamaenerion angustifolium (L.) Scop.
Circaea alpina L.
Epilobium ciliatum Raf.
Epilobium coloratum Biehler
Epilobium leptophyllum Raf.
Epilobium palustre L.
Ludwigia palustris (L.) Elliott [*RDR253*]
Oenothera biennis L.
Oenothera parviflora L. [*SF1409*; *RDR304*]
Oenothera perennis L.

ORCHIDACEAE
Arethusa bulbosa L.*
Calopogon tuberosus (L.) Britton, Sterns & Poggenb.
Corallorhiza maculata (Raf.) Raf.
Cypripedium acaule Aiton
Epipactis helleborine (L.) Crantz [*SF1923*]
Goodyera oblongifolia Raf.
Goodyera tesselata Lodd.
Platanthera aquilonis Sheviak
Platanthera clavellata (Michx.) Luer
Platanthera huronensis (Nutt.) Lindl.*
Pogonia ophioglossoides (L.) Ker Gawl.

OROBANCHACEAE
Epifagus virginiana (L.) W.P.C. Barton [*RDR174*]
Melampyrum lineare Desr.
Rhinanthus minor L. [*RDR121*]

OXALIDACEAE
Oxalis montana Raf. [*RDR163*]
Oxalis stricta L.

PAPAVERACEAE
Dicentra cucullaria (L.) Bernh.

PHRYMACEAE
Erythranthe geyeri (Torr.) G.L. Nesom (=*Mimulus glabratus* (Bentham) Grant)
Mimulus ringens L.

PLANTAGINACEAE
Callitriche palustris L.
Chelone glabra L.
Gratiola neglecta Torr.*
Hippuris vulgaris L.
Plantago lanceolata L. [*RDR279*]
Plantago major L.
Plantago rugelii Decne.
Veronica beccabunga var. americana L. [*RDR263*]
Veronica officinalis L. [*RDR181*]
Veronica serpyllifolia L. [*RDR295*]
Veronica verna L.*

POACEAE
Agrostis gigantea Roth [*RDR129*]

Agrostis scabra Willd. [*RDR248]*
Avenella flexuosa (L.) Drejer
Brachyelytrum aristosum (Michx.) P. Beauv. ex Trel.
Bromus ciliatus L.
Bromus inermis Leyss.
Calamagrostis canadensis (Michx.) P. Beauv.
Cinna latifolia (Trevis. ex Goepp.) Griseb.
Dactylis glomerata L.
Danthonia compressa Austin [*RDR261*; *SF1932*]
Deschampsia cespitosa (L.) P. Beauv.*
Dichanthelium implicatum (Scribn.) Kerguelen [*RDR242*]
Elymus repens (L.) Gould
Elymus smithii (Rydb.) Gould
Festuca saximontana Rydb. [*RDR 185*]
Festuca trachyphylla (Hack.) Hack.*
Glyceria borealis (Nash) Batch.
Glyceria canadensis (Michx.) Trin. [*RDR142*]
Glyceria striata (Lam.) Hitchc.
Leersia oryzoides (L.) Sw. [*SF1934*]
Lolium arundinaceum (Schreb.) Darbysh.
Lolium perenne L.
Milium effusum L.
Muhlenbergia mexicana (L.) Trin.
Oryzopsis asperifolia Michx.*
Panicum capillare L. [RDR269]
Phalaris arundinacea L.
Poa alsodes A. Gray
Poa annua L.
Poa palustris L.
Poa pratensis L. [*RDR232*]
Schizachne purpurascens (Torr.) Swallen*
Setaria pumila (Poir.) Roem. & Schult.
Sphenopholis intermedia (Rydb.) Rydb. [*RDR249*]
Torreyochloa fernaldii (Hitchc.) Church [*RDR147*]

POLYGALACEAE
Polygala paucifolia Willd.*

POLYGONACEAE
Fallopia cilinodis (Michx.) Holub
Persicaria amphibia (L.) Delarbre
Persicaria hydropiper (L.) Delarbre
Persicaria lapathifolia (L.) Delarbre
Persicaria punctata (Elliott) Small
Polygonum douglasii Greene
Rumex acetosella L.
Rumex britannica L.
Rumex obtusifolius L.

PONTEDARIACEAE
Heteranthera dubia (Jacq.) MacMill. [*RDR252*]

POTAMOGETONACEAE
Potamogeton alpinus Balb.
Potamogeton amplifolius Tuck.
Potamogeton confervoides Rchb. [*RDR111*]
Potamogeton epihydrus Raf. [*RDR250*]

Potamogeton friesii Rupr.
Potamogeton natans L.
Potamogeton obtusifolius Mert. & W.D.J. Koch*
Potamogeton praelongus Wulfen*
Potamogeton pusillus L. [*RDR265*]
Potamogeton richardsonii (A. Benn.) Rydb. [*RDR305*]
Potamogeton robbinsii Oakes
Potamogeton zosteriformis Fernald [*RDR254*]
Stuckenia pectinata (L.) Börner

Primulaceae (=Myrsinaceae)
Lysimachia borealis (Raf.) U.Manns & Anderb. (=*Trientalis borealis* Raf.)
Lysimachia terrestris (L.) Britton, Sterns & Poggenb.
Lysimachia thyrsiflora L.

Ranunculaceae
Actaea pachypoda Elliott*
Actaea rubra (Aiton) Willd.*
Anemone canadensis L
Anemone quinquefolia L. [*RDR236*]
Aquilegia canadensis L.*
Caltha palustris L.
Clematis virginiana L.
Coptis trifolia (L.) Salisb. [*RDR161*]
Ranunculus abortivus L.
Ranunculus acris L.
Ranunculus hispidus Michx.
Ranunculus pensylvanicus L.f. [*RDR244*]
Ranunculus recurvatus Poir.
Thalictrum dasycarpum Fisch. & C.A.Mey. & Avé-Lall

Rhamnaceae

Rhamnus alnifolia L’Her. [*RDR257*]

Rosaceae
Agrimonia gryposepala Wallr.
Agrimonia striata Michx.*
Amelanchier arborea (F. Michx.) Fernald
Amelanchier bartramiana (Tausch) M. Roem.
Amelanchier laevis Wiegand*
Aronia prunifolia (Marshall) Rehder [*RDR195*]
Comarum palustre L.
Fragaria virginiana Mill.
Geum aleppicum Jacq.
Geum macrophyllum Willd.
Geum rivale L.*
Malus domestica (Suckow) Borkh. (=*Malus pumila* Mill.) [*RDR233*]
Potentilla argentea L.
Potentilla norvegica L.
Potentilla recta L.*
Potentilla simplex Michx. [*RDR258*]
Prunus pensylvanica L.*
Prunus serotina Ehrh. [*RDR193*]
Prunus virginiana L.
Rosa arkansana Porter
Rosa palustris Marshall

Rubus allegheniensis Porter
Rubus canadensis L. [*RDR180*]
Rubus strigosus Michx. [*RDR179*]
Rubus nutkanus Moc. ex. Ser. (=*Rubus parviflorus* Nutt.)*
Rubus pubescens Raf. [*RDR297*]
Rubus setosus Bigelow
Sibbaldiopsis tridentata (Aiton) Rydb.
Sorbus americana Marshall
Sorbus decora (Sarg.) C.K. Schneid.

RUBIACEAE
Galium asprellum Michx.
Galium tinctorium L.
Galium trifidum L. [*RDR231*]
Galium triflorum Michx.
Mitchella repens L.

SALICACEAE
Populus balsamifera L. [*RDR283*]
Populus grandidentata Michx.
Populus tremuloides Michx. [*RDR285*]
Salix bebbiana Sarg.
Salix discolor Muhl.
Salix humilis Marshall [*RDR286*]
Salix interior Rowlee (=*Salix exigua* Nutt.)
Salix lucida Muhl.
Salix pedicellaris Pursh
Salix petiolaris Sm.
Salix pyrifolia Andersson

SANTALACEAE
Arceuthobium pusillum Peck [*RDR148*]

SAPINDACEAE
Acer pensylvanicum L.
Acer platanoides L. [*RDR197*]
Acer rubrum L. [*RDR176*]
Acer saccharum Marshall [*RDR171*]
Acer spicatum Lam.*

SARRACENIACEAE
Sarracenia purpurea L.

SAXIFRAGACEAE
Chrysosplenium americanum Schwein. ex Hook. [*RDR143*]
Micranthes pensylvanica (L.) Haw.

SCHEUCHZERIACEAE
Scheuchzeria palustris L.

SCROPHULARIACEAE
Scrophularia lanceolata Pursh [*RDR303*]
Verbascum thapsus L. [*RDR287*]

TYPHACEAE
Sparganium americanum Nutt.
Sparganium eurycarpum Engelm.

Sparganium natans L.
Typha latifolia L.

URTICACEAE
Urtica gracilis Aiton (=*Urtica dioica* L.)

VERBENACEAE
Verbena hastata L.

VIBURNACEAE (=ADOXACEAE)
Sambucus canadensis L.
Sambucus racemosa L.
Viburnum cassinoides L. [*RDR302*]
Viburnum trilobum Marshall*

VIOLACEAE
Viola blanda Willd.
Viola cucullata Aiton
Viola lanceolata L. [*RDR136*]
Viola macloskeyi F.E. Lloyd*
Viola renifolia A. Gray*
Viola sororia Willd.

XYRIDACEAE
Xyris montana Ries

SPATIAL VARIATION IN FLOWERING AGE IN *CIRSIUM PITCHERI*: DOES THIS IMPERILED DUNE THISTLE HEDGE ITS BETS?

Lucas A. Priemer[1] and E. Binney Girdler
Department of Biology, Kalamazoo College, Kalamazoo, Michigan

ABSTRACT

For perennial plants, the optimal timing of flowering is a tradeoff between survivorship and fecundity, a classic example of bet-hedging. For many monocarpic perennials, there is an advantage in delaying flowering until the plant reaches a larger size and is thus capable of a higher fecundity. However, in delaying flowering, there is a risk that the plant will die before ever reproducing. Here, we investigate this fitness trade-off in the imperiled dune thistle, *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray (Asteraceae) (Pitcher's thistle). Using a long-term, spatially explicit demographic data set with yearly censuses, we found that *C. pitcheri* individuals on the foredune flowered at a younger age compared to individuals in other dune habitats. We tested two alternative hypotheses: (1) younger flowering plants were able to reach a flowering threshold size more quickly, and (2) these plants were somehow stressed, and slow growth was a signal for high likelihood of dying, resulting in early reproduction at a smaller size. Our results support the former hypothesis: plants in all areas of the dune did not differ in size the year prior to flowering, despite spatial differences in age of flowering individuals. Therefore we conclude that the foredune microenvironment where plants flowered at younger ages facilitates rapid growth and reproduction for this species and may represent optimal habitat. This result provides insight into the demographic patterns of *C. pitcheri* that may inform the conservation and recovery of this threatened species. Although adapted to the dynamic dune environments of the Great Lakes, *C. pitcheri* may be vulnerable to climate change-induced changes in its optimal foredune habitat.

KEYWORDS: Pitcher's thistle, endangered plant species, coastal sand dunes, life history theory, demography.

INTRODUCTION

For flowering plants, the timing of reproduction is an important fitness component. There is a rich literature exploring the costs and benefits of delaying reproduction (Bell 1980; Roff 1992; Metcalf et al. 2003). For monocarpic (semelparous) plants, many factors may influence the timing of bolting, including environmental factors such as water and nutrient availability, climate, or the size and age of the plant (Metcalf et al. 2003).

Many studies have shown that plants have phenotypic plasticity in the timing at which they flower in response to an outside factor. For example, Klinkhamer et al. (1991) studied the effects of environmental factors on the growth and flowering of the monocarpic perennial species *Carlina vulgaris* L.. The results showed that for large individuals, a cold period reduced the number of days it

---

[1] Author for correspondence (lap11902@gmail.com)

took for the plants to flower; without cold treatment, individuals did not flower until reaching a very large size or after many days of enduring long periods of light exposure. In addition, that study posited evidence that plants can respond quite strongly to environmental stimuli.

In evolutionary biology, the conservative bet-hedging strategy is described as the process of risk avoidance on the individual level (Childs et al. 2010). In the case of monocarpic perennial plants, the act of flowering negates the possible future risk of death and is an example of this conservative evolutionary strategy. Although the plant may receive the benefit of a possible increase in fecundity after a year of growth, a plant also faces the risk of death during the following year. Because of this, the act of flowering for these plants is a conservative strategy as it ensures the reproductive success of the plant. Plant species must flower within the optimal timing of reaching the correct benchmark size for maximum reproductive output, but it is difficult to determine this exact size given the variability of most environments.

Some perennial plants have a threshold size that the plant must reach when it has accumulated sufficient resources needed for bolting and flowering (Wesselingh et al. 1997). By delaying flowering until the plant reaches a larger size, a plant is thereby capable of a higher fecundity. However, in delaying flowering, there is an additional risk that the plant will die before reproducing. Lacey (1986) found that a slow growth rate can induce flowering in the short-lived monocarpic perennial *Daucus carota* L.. Metcalf et al. (2003) describe this relationship as “the law of diminishing returns,” in which the payoff of increased fecundity will diminish as a plant’s growth stops or slows after reaching a certain size, after which they will flower. Depending on resources available to plants within their habitats, there is a resulting variation in the age at flowering due to variation in the time that it takes plants to reach the threshold size for bolting. Through a similar demographic study, Kuss et al. (2008) determined that *Campanula thyrsoides* L., a long-lived perennial species endemic to forested areas, exhibited a similar strategy whereby these plants showed a decreasing rate of growth as size increased as well as a pronounced threshold size at which the plants flowered. Additionally, Hanzawa and Kalisz (1993) determined that *Trillium grandiflorum* (Michx.) Salisb., another perennial endemic to wooded areas, flowered only after meeting a threshold leaf area or rhizome volume and that for that species, plant size was a much better indicator for the timing of flowering than a plant’s age.

Nevertheless, it has been shown that for some plant species, there can be variation within a population in both the size and age at which a plant flowers depending on nutrient availability or other environmental factors (Kagaya et al. 2009). This occurs as a result of variable growth rates in response to nutrient availability. For some plants, especially those with high nutrient availability, there can be great plasticity in the size at bolting and flowering. For these species, there is less evidence for a threshold flowering size; the timing of flowering is not dependent on size.

The subject of the present study, *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray (Asteraceae), commonly known as Pitcher’s thistle, is a U.S.A. federally-listed threatened native plant, endemic to the dunes of the western Great Lakes

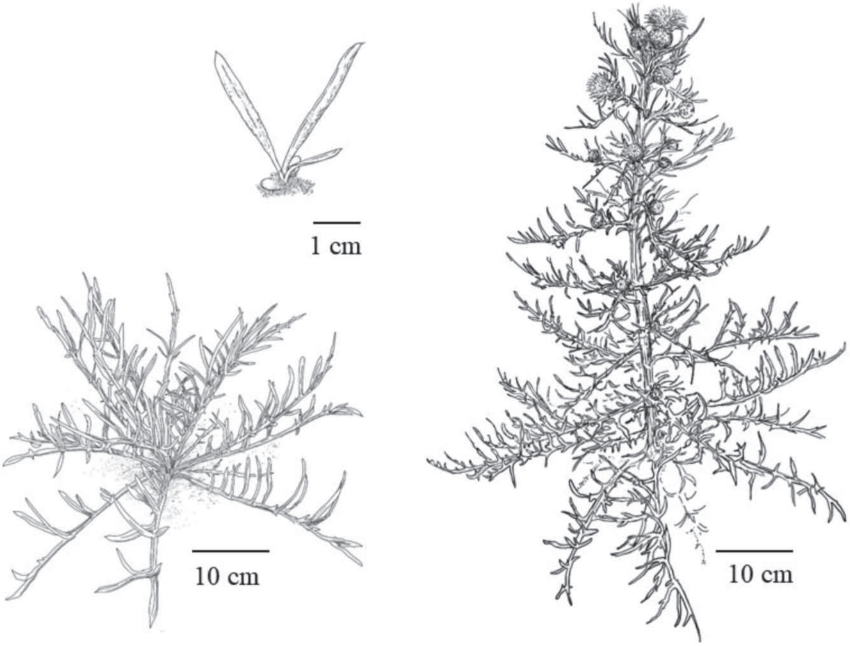

FIGURE 1. The three life stages of *Cirsium pitcheri* tracked in the demographic monitoring plot: (top left) seedling; (bottom left) large vegetative rosette; (right) flowering plant. Drawing by E. Binney Girdler.

shores, where it colonizes open sandy areas maintained by cyclic natural disturbance processes (Pavlovic et al. 2002). Optimal habitat includes both simple linear dunes consisting of a single ridge of sand between the lake and forest, as well as extensive perched dunes and blowouts extending hundreds of meters from the lake shore, such as at Sleeping Bear Dunes National Lakeshore on Lake Michigan. The species is emblematic of coastal dunes in Lake Michigan and Lake Huron, and plays an important role in the dune ecosystem. In particular, its relatively early flowering phenology may be critical for pollinator communities on the dunes (Jolls et al. 2019). Plants live for four to eight years as non-flowering vegetative rosettes, then flower once and die (Loveless 1984; McEachern 1992) (Figure 1).

Our study examines the effect spatial variation may have on the timing and size of flowering on *Cirsium pitcheri* within the dune system. Because of the dynamic nature of the dune environment and the strong elevation and disturbance gradient from the shoreline to the forest (Maun and Perumel 1999), plants living even a small distance apart can be exposed to quite different nutrient and water availability in addition to being affected much differently by climate-related factors (Lichter 1998, 2000). Using a long-term demographic data set, we explored spatial variation in age at flowering across a dune gradient and asked whether early-flowering plants were doing well or hedging their bets. We used size data to test two hypotheses: (1) the younger-flowering plants had ample resources, causing them to be able to reach a flowering threshold size more quickly, or (2) these plants grew slowly and thus had a higher likelihood of dying, resulting in early reproduction at a smaller size.

MATERIALS AND METHODS

Demographic data have been collected annually from 2006 to 2022 in a 40 × 50 m plot located on the shores of Sturgeon Bay on Lake Michigan, Wilderness State Park, Emmet Co., Michigan, USA (45.72°, –84.94°). The plot was established by Dr. Claudia Jolls and her students and has served as the basis of many publications (Havens et al. 2012; Jolls et al. 2015) (Figure 2). One of us (EBG) took over sampling the plot starting in the summer of 2020 to continue the long-term demographic data collection; both LAP and EBG collected data during the summer of 2023 (although that year of data is not included in our analysis). The plot includes a gradient of elevation typical of linear dune systems in the Great Lakes and elsewhere including foredune (dune slopes facing the lake) and backdune (slopes facing inland). From 2006, the plot has been subdivided into 20 smaller 10 × 10 m areas to better keep track of plants in the field. For the current analysis, we divided the larger plot into five zones to capture the gradient of slope and elevation from the shoreline inland. Each zone is 10 m × 40 m oriented with the longer axis parallel to the lakeshore (Figure 2). The zones differ in aspect (Zones 1, 2, and 3 face west; Zones 4 and 5 face east), slope (Zones 3 and 4 are steepest), and vegetative cover (Zones 1 and 2 are more sparsely vegetated). The difference in elevation from the toe (front of Zone 1) to the top of the dune (boundary between Zones 3 and 4) is about three meters (Figure 2; see elevation profile inset). *Ammophila breviligulata* Fern. (Poaceae) (American beachgrass) dominates Zones 1 and 2. It is still prevalent on the dune ridge (Zones 3 and 4) and to a lesser extent on the back dune (Zone 5), co-occurring with patches of *Asclepias syriaca* L. (common milkweed), *Salix* spp. (Salicaceae) (willows), *Juniperus communis* L. (Cupressaceae) (juniper), *Prunus pumila* L. (Rosaceae) (sand cherry), and *Arctostaphylos uva-ursi* (L.) Spreng. (Ericaceae) (bear-berry).

Demographic data analyzed here were collected annually in late June and early July from 2006 to 2022 in each zone. Individuals were followed through time by using numbered ID stamps on metal tags affixed to *Cirsium pitcheri* individuals by vinyl-coated wire. Plant size was measured as taproot diameter (mm) just below the crown (also called root crown diameter) on non-flowering *C. pitcheri* plants.

For the following analyses, we employed custom R scripts in RStudio (R Core Team 2023), utilizing in-house coding procedures tailored to our specific analytical requirements. For the flowering size and age analysis, we selected flowering plants from the 17-year dataset whose entire lifespan was known, i.e, plants first tagged as seedlings and followed until their flowering year, a total of 296 plants. Sample sizes in the Zones 1 through 5 are 23, 179, 33, 43, and 18 plants, respectively. For all models, the size variable, taproot diameter, was natural log-transformed.

Our measure of the fecundity of each plant was the number of capitula (flowering heads). We determined both the age at flowering and the size of vegetative plants the year before they flowered; plants were not measured after they had bolted, since taproot diameter tends to shrink when plants invest resources into the flowering stalk. To quantify the effect of size on the probability of flowering, we selected all instances of a vegetative plant in year t that survived to year t+1 (n = 951 transitions of 296 unique plants; a plant will be represented more than once since each has 2 to 12 transition years). We estimated the probability of flowering in year t+1 (a binary variable, 0 or 1) as a function of ln (taproot diameter in year t) (fixed effect) using a linear model fit by maximum likelihood with Laplace approximation and a binomial (logit) distribution using the lme4 package (Bates et al. 2015) in RStudio (R Core Team 2023). A mixed model with 'zone' as a random effect was not deemed a superior fit, as indicated by the Akaike Information Criterion (AIC). The AIC is a measure that balances model goodness-of-fit with complexity (Burnham and Anderson, 2002). In our context, AIC_{full} represents the AIC for the full model with zone as a random effect, while $AIC_{reduced}$ corresponds to the AIC for the reduced model, with no zone term. The difference (AIC_{full} –

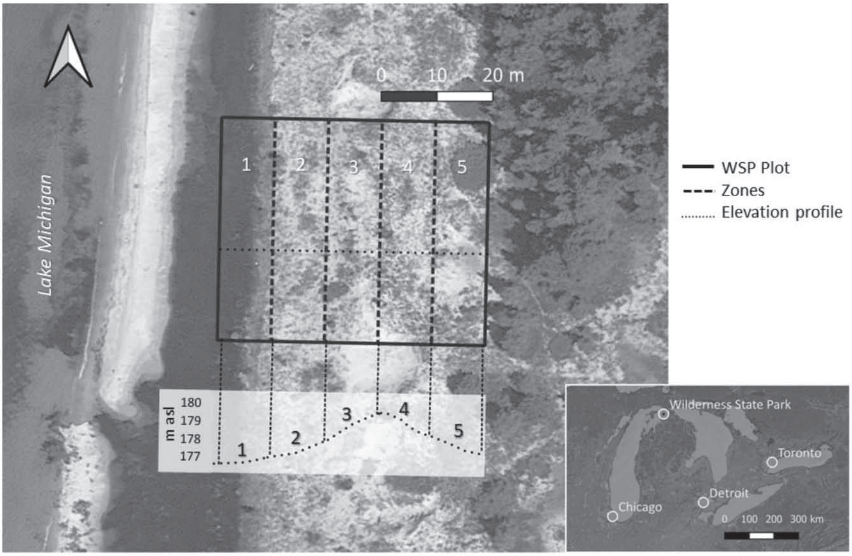

FIGURE 2. Location of the demographic monitoring plot at Wilderness State Park, Emmet County, Michigan (inset shows location within the Great Lakes region) indicated by the solid rectangle, divided into five zones, indicated by dashed lines. Each zone is 10m × 40m oriented with long axis parallel to the lakeshore. The elevation difference from the toe to the top of the dune is approximately three meters. Elevation of Lake Michigan in the 2019 Google Earth satellite image is approximately 177 m.

$AIC_{reduced}$) was less than 2; in other words, the simpler model was more favorable, indicating a relatively better fit without sacrificing explanatory power. To determine the significance of this reduced model, we fit an even more reduced model with only an intercept term, and utilized a chi-square test to compare the deviance of those two models.

We then analyzed the spatial variation in flowering age (years) and natural log-transformed (ln) size in year t (taproot diameter, mm) using general linear models in R (R Core Team 2023) with zone (factor with 5 levels) as the explanatory variable, using Analysis of Variance to determine significance. Following the assessment of main effects through linear model ANOVAs, we conducted pairwise Tukey Honestly Significant Difference (HSD) tests to discern specific differences between zones.

We estimated the relative growth rate (RGR) as ln (taproot diameter at year t+1) – ln (taproot diameter at year t). We combined the yearly transitions between vegetative stages for all plants, resulting in a sample size of 914 data points representing growth from one year to the next for 291 unique plants (note: these were plants that did not flower in year t+1). To test for an expected relationship of RGR with size, we used a linear model of RGR as a function of ln (taproot diameter in year t). Similar to the flowering probability model described above, a simple model without a random zone effect had a relatively better fit ($AIC_{full} – AIC_{reduced}) < 2$.

To test for the expected relationship between fecundity and size, we used a linear model of ln (number of flowering heads in year t+1) as a function of ln (taproot diameter in year t) as a fixed effect and location on the dune (zone) as a random effect using the lme4 package (Bates et al. 2015). In this case, ($AIC_{full} – AIC_{reduced}) > 2$, so we retained the random “zone” effect in the model. For the fecundity model, we omitted four plants with > 25 flowering heads as outliers because they were likely the result of multi-stalked individuals, damaged when they were vegetative rosettes, resulting in a final sample size of 292 flowering plants.

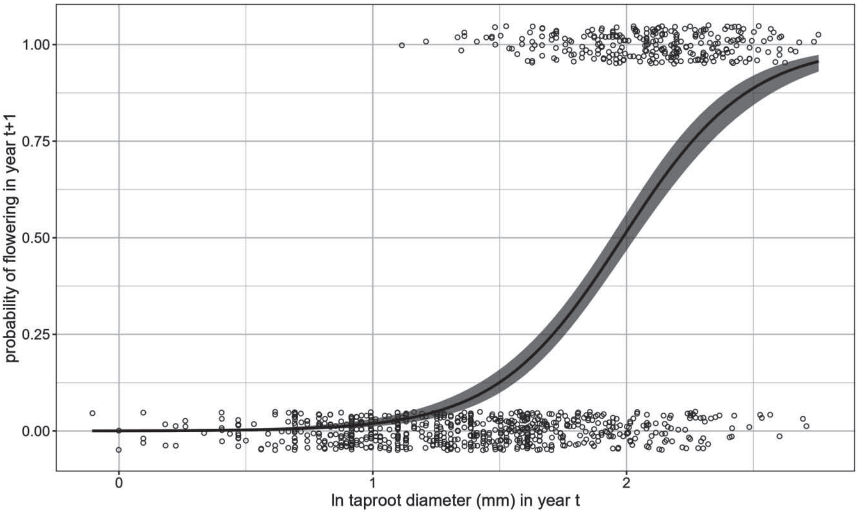

FIGURE 3. The probability of flowering in year t+1 depends on the size of a plant in year t. Shown is the fitted slope of the logistic regression model with a 95% confidence level interval (indicated by the shading surrounding the curve). Each circle is the fate of a single plant; a value of zero indicates the plant did not flower, a one indicates a plant did flower. Circles are jittered around these values to emphasize sample size (n = 951 plant transitions and 296 unique plants).

RESULTS

In the 17-year dataset, we found that the probability of *Cirsium pitcheri* flowering in year t+1 significantly depended on the size of a plant in year t (Figure 3). The logistic regression analysis revealed a significant association between the binary outcome variable (1=flowering, 0 = not) and the natural logarithm of taproot diameter in year t+1, as evidenced by a chi-square test (χ^2 = 431.15, df = 1, $p < 0.0001$), indicating a substantial improvement in model fit compared to the model with just the intercept. In other words, larger plants were much more likely to flower compared to smaller plants.

Overall, *Cirsium pitcheri* plants in our plot ranged in age at flowering from 2 years to 12 years, with a mean (±SD) of 4.6 (±1.45) years. We found spatial variation in the age of flowering plants (One-way ANOVA: $F_{[4]} = 6.508$, $p < 0.0001$) (Figure 4). In particular, plants in Zone 2 flowered on average a full year earlier than plants in the other zones (4.3 years versus 5.3, 5.0, 4.9, and 5.5 years for Zones 1, 3, 4, and 5; Tukey's HSD pairwise p-values: 0.008, 0.059, 0.060, 0.011, respectively) (Figure 4).

However, despite this spatial difference in flowering age, we found no significant differences by zone in the size of plants the year before they flowered (One-way ANOVA: $F_{[4]} = 2.148$, $p = 0.07$) (Figure 5). Tukey's HSD test showed no significant pairwise differences between zones (all pairs $p > 0.3$, except Zone 3 and 4, $p = 0.069$). In particular, plants in Zone 2, although flowering on

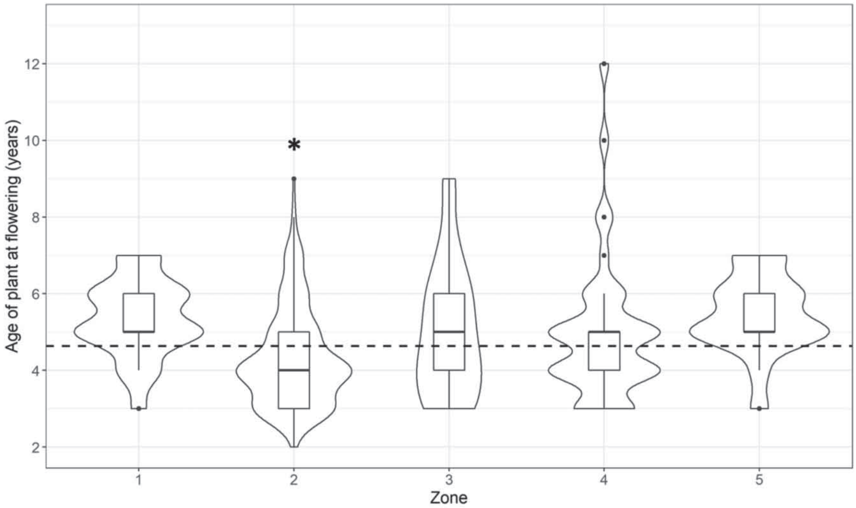

FIGURE 4. The mean age at which plants flower differs by zone (One-way ANOVA: $F_{[4]}$= 6.508, $p < 0.0001$). The widths of the violin plots represent the density or distribution of the data points at different values along the y-axis. A wider section indicates higher data density; more data points fall within that range. Interior box-and-whisker plots show median size as a thick line; the box shows the second and third quartiles, and the two whiskers show the first and fourth quartiles; solid dots indicate outliers. The overall mean age of all plants is shown by the horizontal dashed line. Tukey's HSD test showed that plants in Zone 2 (*) flowered significantly earlier than plants in any of the other zones, which did not significantly differ from each other. Sample sizes in the order of zones are 23, 179, 33, 43, and 18 plants.

average at four years of age, flowered at similar sizes compared to plants that grew an extra year. The mean (±SD) taproot diameter (untransformed) of all flowering plants the year before flowering was about 8.4 (±1.4) mm (Figure 5).

We found that the relative growth rate for *Cirsium pitcheri* at Wilderness State Park was a decreasing function of size in year t. The mean slope for the five zones is – 0.33, which is highly significant ($p < 0.001$, $R^2 = 0.27$); the slopes do not differ by zone (Figure 6). Fecundity, estimated as the number of flowering heads in year t+1, increases with the size of the taproot in year t regardless of zone ($F_{[1, 914]}$= 42.317, $p < 0.001$, Figure 7). Zone further explained variation in flowering heads ($F_{[4, 914]}$=2.4967, $p = 0.0414$); plants in Zone 5 had significantly fewer flowering heads than plants in Zones 2 and 3 (Tukeys HSD, $p < 0.05$). No other pairwise comparisons were significantly different (Tukeys HSD test, $p > 0.05$).

DISCUSSION

Our findings provide support for the first of our alternate hypotheses: *Cirsium pitcheri* plants that flowered a whole year earlier than plants in other zones did

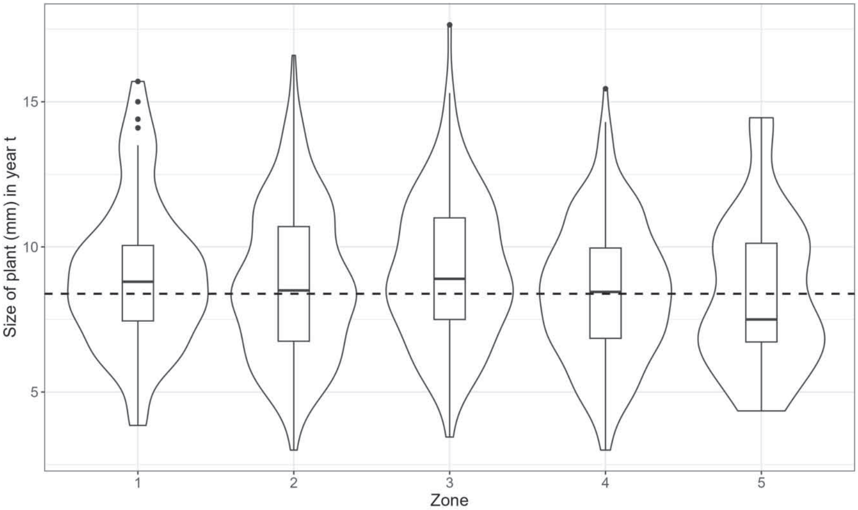

FIGURE 5. The mean size in year t after which plants flower in year t+1 is similar in all zones on the dune (One-way ANOVA: $F_{[4]} = 2.148$, $p = 0.07$). The widths of the violin plots represent the density or distribution of the data points at different values along the y-axis. A wider section indicates higher data density; more data points fall within that range. Interior box-and-whisker plots show median size as a thick line; the box shows the second and third quartiles, and the two whiskers show the first and fourth quartiles; solid dots indicate outliers. The overall mean size of all plants is shown by the horizontal dashed line. Sample sizes in the order of zones are 23, 179, 33, 43, and 18 plants.

so because they reached a threshold flowering size that appears typical of this species, at least at this site. Plants did not flower early as a conservative bet-hedging strategy to avoid the risk of death.

We therefore conclude that there is an optimum threshold size at which *Cirsium pitcheri* appears to flower, and that early-flowering plants did not hedge bets due to poor prospects, at least as indicated by slow growth. Although the literature on this threatened plant notes that the length of the juvenile stage ranges from four to eight years (Loveless 1984; Havens et al. 2012), we here report the first estimate of the flowering size threshold as 8.4 (±1.4) mm. Our long-term comprehensive data set also expands the range of the records for the vegetative juvenile stage for *C. pitcheri* (two to 12 years at Wilderness State Park).

Life history theory for monocarpic plants suggests that a law of diminishing returns applies: if fecundity increases with size but relative growth rate (RGR) decreases with size, the payoff of delayed reproduction gets smaller as the plant grows (Metcalf et al. 2003). Consistent with that expectation, we found that RGR in *Cirsium pitcheri* at our site was a decreasing function of size and that fecundity increased as plants grew larger. Like many other monocarpic perennials, selection has favored a threshold size that will instigate flowering in *C. pitcheri.* Despite within-site variation in age at flowering across the lake-to-forest dune gradient, the size of the plant the year before flowering was

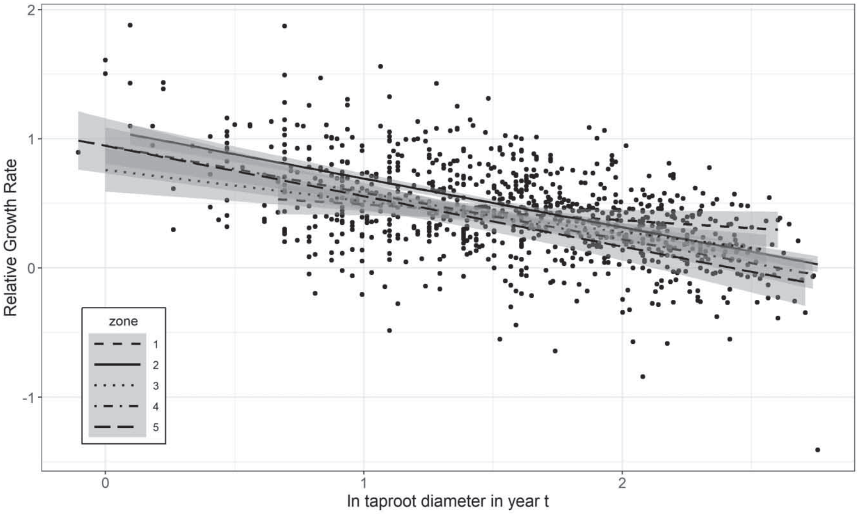

FIGURE 6. Scatter diagram showing the relationship between relative growth rate and the natural log of taproot diameter. Shown are fitted slopes for each zone and a 95% confidence level interval (indicated by the shading surrounding each curve) for linear model predictions, although slopes for zones did not significantly differ. Overall, size was a significant predictor of relative growth rate ($p < 0.001$, $R^2 = 0.27$) The sample size is 296 plants, with 914 data points representing growth transitions between years.

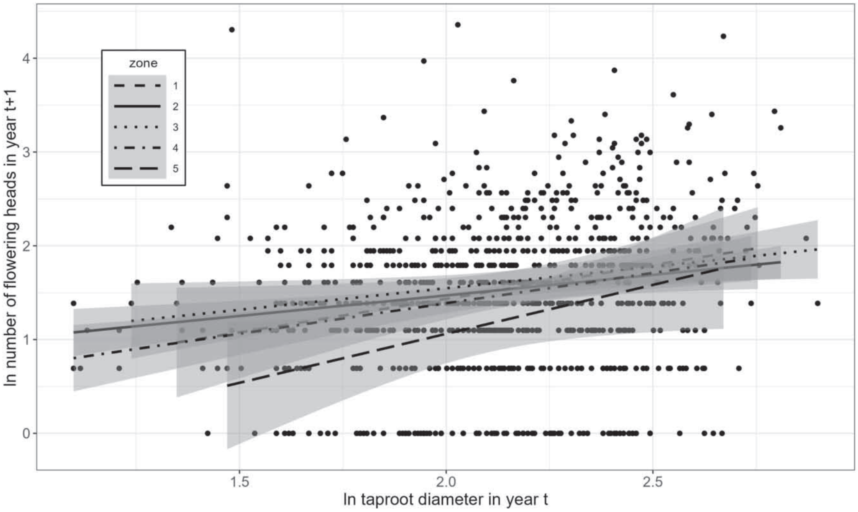

FIGURE 7. Scatter diagram showing the relationship between the number of flowering heads in year t+1 and taproot diameter in year t. Shown are fitted slopes for each zone and a 95% confidence level interval (indicated by the shading surrounding each curve) for linear model predictions. Zones had significantly different slopes ($F_{[4, 914]}$=2.4967, p = 0.0414). Sample size is 292 plants (four outliers were omitted).

consistent. Whether this threshold size for flowering is common across the species' range is unknown. There are several ongoing studies of *C. pitcheri* in the Great Lakes (McEachern et al. 1994; Havens et al. 2012; Rand et al. 2015; Halsey et al. 2016; Nantel et al. 2018); doubtless these authors have data to test for larger scale patterns in flowering age and size.

Future work could also explore whether the threshold size we have identified here (8.4 ± 1.4 mm) results in a theoretical maximum reproductive yield for *Cirsium pitcheri*. There are several methods to predict optimal threshold sizes that will maximize fecundity and fitness, such as integral projection models (Rees and Rose 2002; Williams 2009), and the evolutionarily stable strategy approach (Hesse et al. 2008). Additionally, future studies might investigate how the survivorship of *C. pitcheri* varies with increasing size, particularly how the survival of plants tracks beyond the identified threshold flowering size. Such investigations will inform estimates of generation time, population growth rate, and the likelihood of population persistence in this threatened species.

We conclude that for the Wilderness State Park population, our Zone 2, which encompassed not the newest beach but the first rise of the foredune, comprises a microenvironment where *Cirsium pitcheri* plants grew rapidly and flowered at younger ages and, as such, may represent optimal habitat. This foredune habitat may represent a within-site source population, with the other zones being sinks. Such insight into the spatial demographic patterns of *C. pitcheri* informs the conservation and recovery planning of this threatened species; maintenance of the foredune throughout this threatened species' range may be important to its persistence. Future work should more closely examine *C. pitcheri* vital rates across the dune gradient to determine what environmental factors contribute to variation in success. Paradoxically, it might be active sand movement and burial that stimulates growth (Maun and Perumal 1999). In contrast, such active sand movement might bury competitors and release *C. pitcheri* from competition.

Finally, we note that over the course of this 17-year study, the elevation of Lake Michigan has changed dramatically, with a historic high level of 177.45 m in June 2020 and a low of 175.57 m in January of 2013 (GLISA, 2023), a change of almost two meters. The Great Lakes have fluctuated historically in response to climate, especially to the evaporation-precipitation ratio (McEachern 1992; Gronewald et al. 2013). These coastal processes can greatly affect dune geomorphology. The foredune environment we have identified as optimal habitat for *Cirsium pitcheri* might be at risk of erosion during periods of high lake levels or at risk of excessive sand burial during the period just after high lake levels when exposed sand is blown inland. Indeed, we have seen both processes at Wilderness State Park and other locations from 2019 to 2023. Precipitation and lake levels are projected to increase in response to human-induced climate change. Kayastha et al. (2022) predict that Lake Michigan will experience an average annual increase in water level of 0.44 m above the 2020 high by 2040–2049.

We note, however, that *C. pitcheri* occurs not only on simple linear dunes like our demography plot, but also in discontinuous patches of open sand (blowouts), continuous dune fields, and perched dune systems in the Great Lakes (Loveless 1984; Pavlovic et al. 2002). A range-wide comparison of *C. pitcheri* demography among the various populations in these different habitats will be important to understanding the threats to its long-term persistence and to assessing whether a habitat analogous to our Zone 2 is critical to *C. pitcheri* population viability. It is critical to continue close study of *C. pitcheri* and other dune endemic species and to consider the possibility of management interventions such as assisted dispersal and reintroductions to ameliorate effects of climate change on this sensitive ecosystem.

AUTHOR CONTRIBUTIONS

EBG conceived of this study, LAP and EBG collected the demographic data (along with previous researchers, see acknowledgments). EBG and LAP jointly designed and conducted the analyses and created the figures. LAP drafted the manuscript, and both authors edited and revised the manuscript.

ACKNOWLEDGMENTS

Our long-term demography plot was initiated by Dr. Claudia Jolls of East Carolina University. Permits to work with *Cirsium pitcheri* at Wilderness State Park were obtained from the Michigan Department of Natural Resources, Parks & Recreation Division, Stewardship Unit, Lansing, Michigan, by Claudia Jolls (for the period 2006–2019) and E. Binney Girdler (for the period 2020–2022). We acknowledge recent funding from a US Fish and Wildlife Service Great Lakes Restoration Initiative grant (#F21AC00010-00) to Dr. Kayri Havens, Chicago Botanic Garden, as well as technical support from Dr. Tiffany Knight and Dr. Roxanne Leberger of the German Center for Integrative Biodiversity Research in Leipzig, Germany. Some equipment and lodging in some years was provided by the University of Michigan Biological Station in Pellston, Michigan. Funding for the second author was provided by a Kalamazoo College faculty development grant. We thank the editor and an anonymous reviewer for very helpful suggestions that clarified the presentation of our study.

LITERATURE CITED

Bates, D., M. Mächler, B. Bolker, and S. Walker. (2015). Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Bell, G. (1980). The costs of reproduction and their consequences. American Naturalist 116: 45–76.

Burnham, K. P., and D. R. Anderson. (2002). Model selection and multi-model inference: A practical information-theoretic approach. Springer-Verlag, New York, N.Y.

Childs, D. Z., C. J. E. Metcalf, and M. Rees (2010). Evolutionary bet-hedging in the real world: Empirical evidence and challenges revealed by plants. Proceedings of the Royal Society B: Biological Sciences 277: 3055–3064.

GLISA. (2023). Lake levels overview. Ann Arbor, Michigan. Available at https://glisa.umich.edu/sustained-assessment/lake-levels/. (Accessed July 21, 2023).

Gronewold, A.D., V. Fortin, B. Lofgren, A. Clites, C. A. Stow, and F. Quinn. (2013). Coasts, water levels, and climate change: A Great Lakes perspective. Climatic Change 120: 697–711.

Halsey, S. J., T. J. Bell, K. McEachern, and N. B. Pavolovic. (2016). Population-specific life histories contribute to metapopulation viability. Ecosphere 7(11): e01536.

Hanzawa, F. M., and S. Kalisz. (1993). The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). American Journal of Botany 80: 405–410.

Havens, K., C. L. Jolls, J. E. Marik, P. Vitt, A. K. McEachern, and D. Kind. (2012). Effects of a non-native biocontrol weevil, *Larinus planus*, and other emerging threats on populations of the federally threatened Pitcher's thistle, *Cirsium pitcheri*. Biological Conservation 155: 202–211.

Hesse, E., M. Rees, and H. Müller-Schärer. (2008). Life-history variation in contrasting habitats: Flowering decisions in a clonal perennial herb (*Veratrum album*). The American Naturalist 172(5): E196–E213.

Jolls, C. L., J. E. Marik, S. I. Hamzé, and K. Havens. (2015). Population viability analysis and the effects of light availability and litter on populations of *Cirsium pitcheri*, a rare, monocarpic perennial of Great Lakes shorelines. Biological Conservation 187: 82–90.

Jolls, C. L., J. N. Inkster, B. G. Sholtens, P. Vitt., and K. Havens. (2019). An endemic plant and the plant-insect visitor network of a dune ecosystem. Global Ecology and Conservation 18: e00603.

Kagaya, M., T. Tani, and N. Kachi. (2009). Variation in flowering size and age of a facultative biennial, *Aster kantoensis* (Compositae), in response to nutrient availability. American Journal of Botany 96: 1808–1813.

Kayastha, M.B., X. Ye, C. Huang, and P. Xue. (2022). Future rise of the Great Lakes water levels under climate change. Journal of Hydrology 612: 128205.

Klinkhamer, P. G., T. J. de Jong, and E. Meelis. (1991). The control of flowering in the monocarpic perennial *Carlina vulgaris*. Oikos 61: 88–95.

Kuss, P., M. Rees, H. H. Ægisdóttir, S. P. Ellner, and J. Stöcklin. (2008). Evolutionary demography of long-lived monocarpic perennials: A time-lagged integral projection model. Journal of Ecology 96: 821–832.

Lacey, E. P. (1986). The genetic and environmental control of reproductive timing in a short-lived monocarpic species *Daucus carota* (Umbelliferae). Journal of Ecology 74: 73–86.

Lichter, J. (1998). Primary succession and forest development on coastal Lake Michigan sand dunes. Ecological Monographs 68(4): 487–510.

Lichter, J. (2000). Colonization constraints during primary succession on coastal Lake Michigan sand dunes. Journal of Ecology 88: 825–839.

Loveless, M. D. (1984). Population biology and genetic organization in *Cirsium pitcheri*, an endemic thistle. Ph.D. dissertation, Lawrence: University of Kansas.

Maun, M., and J. Perumal. (1999). Zonation of vegetation on lacustrine coastal dunes: Effects of burial by sand. Ecology Letters 2: 14–18.

McEachern, K. (1992). Disturbance dynamics of Pitcher's thistle (*Cirsium pitcheri*) populations in Great Lakes sand dune landscapes. Ph.D. dissertation, University of Wisconsin-Madison, 215 pp.

McEachern, A. K., M. L. Bowles, and N. B. Pavlovic. (1994). A metapopulation approach to Pitcher's Thistle (Cirsium pitcheri) recovery in southern Lake Michigan dunes. USGS Staff-Published Research 239.

Metcalf, J. C., K. E. Rose, and M. Rees. (2003). Evolutionary demography of monocarpic perennials. Trends in Ecology & Evolution 18: 471–480.

Nantel, P. L., J. Jones, and C. Drake. (2018). Viability of multiple populations across the range of a species at risk: The case of Pitcher's thistle, *Cirsium pitcheri*, in Canada. Global Ecology and Conservation 16: e00445.

Pavlovic, N. B., M. L. Bowles, S. R. Crispin, T. C. Gibson, K. D. Herman, R. T. Kavetsky, A. K. McEachern, and M. R. Penskar. (2002). Pitcher's thistle *Cirsium pitcheri* recovery plan. United States Department of the Interior, United States Fish and Wildlife Service, Minneapolis, Minnesota.

R Core Team. (2023). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.R-project.org/ (Accessed July 20, 2023).

Rand, T. A., S. M. Louda, K. M. Bradley, and K. K. Crider. (2015). Effects of invasive knapweed (*Centaurea stoebe* subsp. *micranthos*) on a threatened native thistle (*Cirsium pitcheri*) vary with environment and life stage. Botany 93: 543–558.

Rees, M., and K. E. Rose. (2002). Evolution of flowering strategies in *Oenothera glazioviana*: an integral projection model approach. Proceedings of the Royal Society of London. Series B: Biological Sciences 269: 1509–1515.

Roff, D. K. (1992). The evolution of life histories. Chapman & Hall, New York, N.Y.

Wesselingh, R. A., P. G. Klinkhamer, T. J. de Jong, and L. A. Boorman. (1997). Threshold size for flowering in different habitats: Effects of size-dependent growth and survival. Ecology 78: 2118–2132.

Williams, J. L. (2009). Flowering life-history strategies differ between the native and introduced ranges of a monocarpic perennial. The American Naturalist 174: 660–672.

NOTEWORTHY COLLECTIONS

NOTABLE RECORDS OF *HOMALOSORUS PYCNOCARPOS* AND *DRYOPTERIS EXPANSA* FOR THE EASTERN UPPER PENINSULA OF MICHIGAN

Scott M. Warner
Conservation Associate, Michigan Natural Features Inventory
Associate, Michigan State University Herbarium
warner91@msu.edu

Michael R. Penskar
15601 Dutton Road
Gregory, MI 48137
penskar@umich.edu

Homalosorus pycnocarpos (Spreng.) Pic. Serm.
Diplaziopsidaceae
Narrow-leaved spleenwort, glade fern

Significance of the Report. The second known record for the eastern Upper Peninsula of Michigan and the third Upper Peninsula record overall; the first since 1965, though there is some ambiguity regarding the location of the 1965 record.

Previous Knowledge. In Michigan, *Homalosorus pycnocarpos* is found in rich, moist deciduous woods, particularly near seeps and small streams and at the base of slopes (MICHIGAN FLORA ONLINE 2011; Palmer 2018). It has a coefficient of conservatism of 10 (Reznicek et al. 2014), indicating a high fidelity to habitat remnants that have remained relatively free of human disturbance since European settlement (Swink and Wilhelm 1994).

This species is known from most states and provinces of eastern North America (NatureServe 2022). According to MICHIGAN FLORA ONLINE (2011), it is known in Michigan from most of the counties in the southern Lower Peninsula, a scattering of counties in the northern Lower Peninsula, and one county in the Upper Peninsula. The Michigan Flora online database contains 69 records of the species. Though not State Threatened, State Endangered, or of Special Concern, this suggests it is relatively uncommon. For comparison, the familiar lady fern (*Athyrium filix-femina*) and spinulose woodfern (*Dryopteris carthusiana*) are represented in the database by 307 and 294 records, respectively. Several of the known localities of *Homalosorus pycnocarpos* are among those most cherished by southern Michigan botanists—Russ Forest, Warren Woods, Sharon

Hollow, Sanford Woodlot, and Brandt Woods—illustrating its affinity for quality habitats.

A search of the Consortium of Midwest Herbaria (2022) database revealed 113 Michigan collections of *Homalosorus pycnocarpos*, including some not found in the MICHIGAN FLORA ONLINE (2011) database. Notably, this includes what would be a Chippewa County record, if verified by the Michigan Flora Project. That collection was made on July 10, 1965 along M-123 along Whitefish Bay north of Paradise (*C. Vander Mark and S. Russell 272*, GVSC). The determination is accurate based on the first author's examination of a digitized image of the herbarium sheet. However, the habitat is noted as "northern white cedar–bog birch seepage" and "Black Creek roadside ditch." This sunny boreal disturbed setting seems inconsistent with the known habitat of *Homalosorus pycnocarpos*: high-quality hardwood forests. Furthermore, the location is listed as "T49N, R6W, Sect. 3 (SE ¼)" and "s. of Paradise," but Section 3 of T49N, R6W is north of Paradise, and it contains not the crossing of M-123 with Black Creek but the crossing of N Whitefish Point Rd. with the Shelldrake River. Though Vander Mark and Russell were active elsewhere in Luce and Mackinac Counties on July 10, 1965, Russell's collection numbers from that day are not sequential: 208–211, 216–217, 261, 272, and 274. Finally, the record within the Consortium of Midwest Herbaria (2022) database is noted as being from Charlevoix County and not, as the herbarium sheet label indicates, Chippewa County. It seems conceivable that some sort of label mixup occurred. Regardless, the present collection was made from Chippewa County, 47 km (29 miles) south-southeast of the reported location of the 1965 collection (i.e., the crossing of M-123 with Black Creek). The other Upper Peninsula record is from Chatham in Alger County in 1900 (MICHIGAN FLORA ONLINE 2011). Suitable habitat does exist near Chatham. No Upper Peninsula observations have been submitted to iNaturalist (2022). The Pteridophyte Collections Consortium (2022) does not list any additional Upper Peninsula collections.

This species has also been known under the following names: *Asplenium pycocarpon* (Spreng.), *Athyrium pycnocarpon* (Spreng.) Tidestr., *Diplaziopsis pycnocarpa* (Spreng.) M.G.Price, and *Diplazium pycnocarpon* (Spreng.) M.Broun, among others.

Discussion. While apparently rare in northern Michigan, particularly in the Upper Peninsula, *Homalosorus pycnocarpos* was found in great abundance at the present site (Figure 1). Even a conspicuous plant growing in abundance can lurk undiscovered in remote areas.

Though at first it appeared that the first author had found a disjunct county record, examination of the Consortium of Midwest Herbaria database (2022) revealed that this may not be the case. Ambiguities about habitat and specific location notwithstanding, it is possible Vander Mark and Russell collected *Homalosorus pycnocarpos* somewhere in Chippewa County, as suitable habitat can be found in much of the county. For example, Vander Mark and Russell collected at Tahquamenon Falls State Park on the same date recorded on the *Homalosorus* sheet, and rich northern hardwoods exist at that state park.

This case study illustrates the importance of databases other than MICHIGAN FLORA ONLINE (2011), as well as the importance of small herbaria.

FIGURE 1. Narrow-leaved spleenwort (*Homalosorus pycnocarpos*) was robust and abundant in an area of about 1/8 ha in a moist slippery elm–silver maple–sugar maple woods in the Hiawatha National Forest 3 km NE of Ozark, Michigan. Photo by Scott M. Warner.

While the Michigan Flora Project is the gold standard for documenting the habitat and distribution of Michigan plants, its agents cannot examine every collection taken from the state. Additional sources can sometimes provide further information. GVSC is home to 3500 specimens (Thiers continuously updated). Had a local herbarium not been available to the collectors of the previous Chippewa County record they might not have collected the specimen. Had the data not been digitized and added to the Consortium of Midwest Herbaria database, the present authors would not have known about the record.

Diagnostic Characteristics. *Homalosorus pycnocarpos* is a large fern, one of Michigan's few ferns with both once-pinnate fronds and entire to crenulate pinnules. Among these few species, it is the only one with sori linear along the veins. It is weakly dimorphic (Figure 2), with the fertile fronds bearing narrower pinnae than those of the sterile fronds (Palmer 2018).

Specimen Citation. MICHIGAN. Chippewa County: Hiawatha National Forest, 1/8 km E of Boaz Lake, 3 km NE of town of Ozark. 46.163378°, –84.931728°. Locally abundant. Covering ca. 1/8 ha with minor satellite patches just beyond. Under sugar maple in moist slippery elm–silver maple–sugar maple woods. Ground associates: *Circaea canadensis*, *Allium tricoccum*, *Sambucus racemosa*, *Fraxinus pennsylvanica*, *Adiantum pedatum*, *Dryopteris carthusiana*,

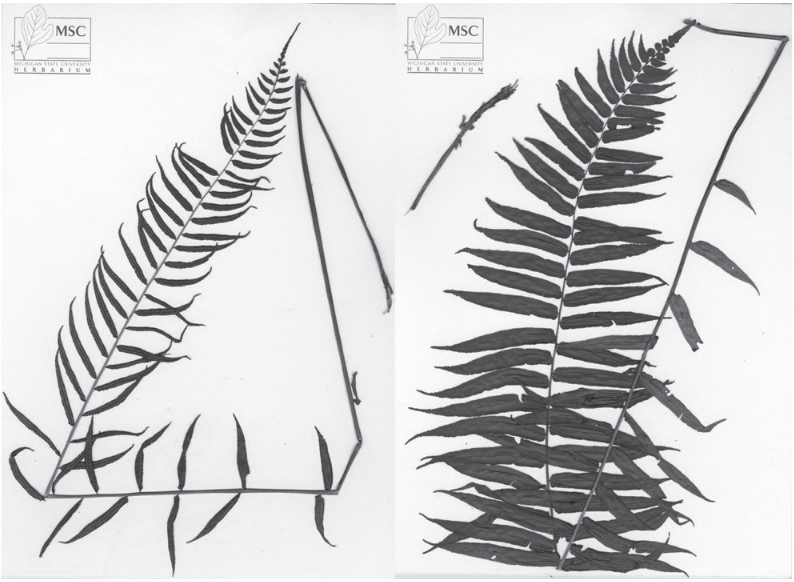

FIGURE 2. Voucher from the present observation of narrow-leaved spleenwort (*Homalosorus pycnocarpos*) prior to mounting. The species shows weak dimorphism between fertile fronds (left) and sterile fronds (right). Photo by Scott M. Warner.

Elymus hystrix, *Rubus occidentalis*, *Rubus strigosus*, *Agrimonia gryposepala*, *Prunus serotina*, *Galeopsis tetrahit*, *Carex intumescens*, and *Athyrium filix-femina.* Vigorous sori production. August 30, 2022, *Scott M. Warner 1190* (MSC; duplicates to be distributed to CMC, MICH, and MSC).

Dryopteris expansa (C. Presl) Fraser-Jenk. & Jermy
Dryopteridaceae
Expanded Woodfern; Spreading Woodfern

Significance of the Report. The first documented record in Michigan's eastern Upper Peninsula, constituting a marked extension of the state range. We also note an additional Mackinac County collection made farther east three months after the record reported here. Though this report is not prompt, there have been no additional collections since 2011, and we hope to stimulate further search efforts by reporting these collections.

Previous Knowledge. *Dryopteris expansa* (C. Presl) Fraser-Jenk. & Jermy is a distinctive boreal woodfern known previously in Michigan from five counties in the western Upper Peninsula (including records in Keweenaw County from both mainland and Isle Royale National Park), where it occurs in northern hardwood forests, mixed northern hardwoods, and pine forests (MICHIGAN FLORA ONLINE 2011). More specifically, as detailed by Palmer (2018), in Michigan this species is found in cool moist woodlands, and especially near or at the base of rocky slopes, in canyons, and in shaded, damp ravines, and not uncommonly near the edge of shrubby wetlands and along wooded shorelines. It has a high coefficient of conservatism rank of 9 (Reznicek et al. 2014), indicating a strong association with high quality habitats remaining relatively intact following European migration and settlement.

Dryopteris expansa is a circumboreal species, occurring broadly in two large areas of North America (NatureServe 2022). In the northeast, it ranges from the upper Midwest (in the northern regions of Minnesota, Wisconsin, and Michigan) northeast through northern Ontario and northern Quebec into Newfoundland and Labrador and extending to the extreme southwestern edge of Greenland. In western North America this species ranges from southern and western Alaska to central coastal California, where it appears to occur primarily in cool moist woods and on rocky slopes (Montgomery and Wagner 1993). MICHIGAN FLORA ONLINE (2011) lists a total of 42 collections of *Dryopteris expansa* and an additional 15 collections determined to be hybrids between *D. expansa* and the more common and widespread woodferns *D. marginalis* (five collections) and *D. intermedia* (ten collections).

Discussion. Although no longer listed as a Special Concern species in Michigan, *Dryopteris expansa* is nevertheless a relatively uncommon species. We suspect that, based on our current knowledge of the distribution and on the type of habitat available, this species is at least somewhat overlooked, especially in the forested terrain of the central and eastern Upper Peninsula where there is considerable potential for it to occur. A notable feature of its distribution in Michigan is that the vast majority of collections are from Marquette (18) and Keweenaw (12) Counties, which comprise 71% of collections. Furthermore, there is only one mainland collection in Keweenaw County, as 11 of the 12 records derive from island collections (nine from the Isle Royale Archipelago and two from Manitou Island). Interestingly, there is no record of this species from Houghton County, which comprises the largest area on the Keweenaw Peninsula and extends considerably inland, and only two records are known from each of Ontonagon County and Baraga County, which likely have significant amounts of potential habitat for *D. expansa*.

A population of *Dryopteris expansa* was discovered on June 21, 2011 by the second author during biological surveys of the eastern unit of the Hiawatha National Forest with Michigan Natural Features Inventory colleague David Cuthrell. The new location, which is in Mackinac County, extends the known range of this species in the Upper Peninsula by about 216 km (134 miles) eastward. The initial determination was confirmed by Anton Reznicek in 2014. A subsequent collection of this species was made on September 24, 2011 by Will MacKinnon 16 km (10 miles) east of the initial county discovery. In a 2011 determination, Robert Preston asserts that the initial determination was likely correct, however the possibility of the specimen being a hybrid cannot be ruled out. Based on these discoveries, we suggest that there is widespread habitat for this species throughout the Upper Peninsula and that it is possible that *D. expansa* may be present in the northern Lower Peninsula as well. Unlike most homosporous ferns, *D. expansa* has the ability to self-fertilize (Soltis and Soltis 1987).

Thus, if a single spore disperses and germinates a long distance from the sporophyte, a single gametophyte can theoretically lead to a viable population.

Woodferns are widespread in Michigan and are classic "look-alikes," often not easily distinguished, and thus the genus *Dryopteris* is a legitimately challenging group. Identification may be further complicated by a tendency to hybridize, as discussed and well-illustrated by Carlson (1979). *Dryopteris expansa*, however, has some distinctive if not very striking features, as detailed below, that are well described and illustrated in the thorough modern treatment of Michigan's ferns and lycophytes of Palmer (2018).

Diagnostic Characters. *Dryopteris expansa* is a relatively large, clump-forming, and broad-leaved woodfern with very dense scales on the lower portion of the leaf rachis. Although superficially similar to *D. marginalis* or *D. intermedia*, with which it may commonly occur, it can be distinguished from them by the large striking downward-pointing pinnules adjacent to the rachis on the lower side of the basal pinnae. These large lower (basioscopic) pinnules are in strong contrast to the two smaller (acroscopic) pinnules immediately above and are also attached noticeably farther from the leaf rachis (Palmer 2018).

Specimen Citations. MICHIGAN. Mackinac County: T43N R4W Sec 22. Lat: 46.10326°, Long: –84.79288°. Very local, only a few stems noted, occurring in second-growth mesic northern forest dominated by *Acer saccharum*, *Tilia*, and *Fraxinus*. *Penskar 1537 and Cuthrell*, June 21, 2011 (MICH). T43N R2W Sec. 20. Lat: 46.103402°, Long: –84.58896°. Gentle NW slope in wet-mesic to mesic mixed hardwood stand in transition to lowland conifer. *Acer rubrum*, *Betula papyrifera*, *Acer saccharum*, *Abies balsamea*, *Corylus cornuta*, *Aralia nudicaulis*, *Oryzopsis asperifolia*, *Cornus canadensis*, *Huperzia lucidula*, *Oxalis acetosella*. *William A. MacKinnon 2983*, Sept. 24, 2011 (MICH).

AUTHOR CONTRIBUTIONS

SMW and MRP independently discovered and collected the *Homalosorus* and *Dryopteris* records, respectively, and decided to combine the reports. Each species report was primarily written by the collector of that species. Both authors contributed ideas and revisions to the entire manuscript.

ACKNOWLEDGMENTS

We wish to thank the Hiawatha National Forest for providing support for Michigan Natural Features Inventory to conduct biological surveys on the forest, and we are grateful to the volunteers and staff at MSC and MICH for curating our specimens and generously allowing use of their facilities; Matt Chansler was particularly helpful. We appreciate the trenchant suggestions from editor Michael Huft and two anonymous reviewers, which substantially strengthened the article. We commend Will MacKinnon for his discovery of a second eastern Upper Peninsula population of *D. expansa*.

LITERATURE CITED

Carlson, T. J. (1979). The comparative ecology and frequencies of interspecific hybridization of Michigan woodferns. The Michigan Botanist 18: 47–56.

Consortium of Midwest Herbaria. 2022. Available at https://midwestherbaria.org/portal/index.php (Accessed December 8, 2022).

iNaturalist. (2022). Available at https://www.inaturalist.org. Accessed November 17, 2022.

MICHIGAN FLORA ONLINE. A. A. Reznicek, E. G. Voss, and B. S.Walters. January (2011). University of Michigan. Available at http://michiganflora.net/home.aspx (Accessed December 8, 2022).

Montgomery, J. D., and W. H. Wagner, Jr. (1993). *Dryopteris*. Pp. 280–288 in Flora of North America. Volume 2: Pteridophytes and Gymnosperms. Flora of North America Editorial Committee, editors. Oxford University Press, New York, N.Y. Available online at http://beta.floranorthamerica.org. Accessed (December 14, 2022).

NatureServe. (2022). NatureServe Network Biodiversity Location Data accessed through NatureServe Explorer (web application). NatureServe, Arlington, Virginia. Available at https://explorer.natureserve.org/. (Accessed November 17, 2022).

Palmer, D. D. (2018). Michigan ferns and lycophytes: A guide to the species of the Great Lakes region. University of Michigan Press, Ann Arbor.

Pteridophytes Collections Consortium (2022). Available at https://www.pteridoportal.org/. (Accessed November 17, 2022).

Soltis, D. E. and P. S. Soltis. (1987). Breeding system of the fern *Dryopteris expansa*: Evidence for mixed mating. American Journal of Botany. 74: 504–509.

Swink, F., and G. Wilhelm. (1994). Plants of the Chicago Region, 4th edition. Indiana Academy of Science, Indianapolis.

Reznicek, A. A., M. R. Penskar, B. S. Walters and B. S. Slaughter (2014). Michigan floristic quality assessment database. Herbarium, University of Michigan. Available at https://michiganflora.net/home.aspx (Accessed November 15, 2022).

Thiers, B. (continuously updated). Index herbariorum: A global directory of public herbaria and associated staff. Available at http://sweetgum.nybg.org/ih/ (Accessed November 17, 2022).

BOOK REVIEW

Adam P. Karremans. 2023. *Demystifying Orchid Pollination: Stories of Sex, Lies and Obsession*. Royal Botanic Gardens, Kew. 442 pp., hardcover $50.00. ISBN 978-1842467-84-8; eBook $50.00. ISBN 978-1842467-85-5.

There is something alluring about orchids that has captured the attention of naturalists and plant enthusiasts for over 100 years. This has been highlighted more recently in books such as Susan Orlean's bestselling *The Orchid Thief: A True Story of Beauty and Obsession* (Orlean 1998) and Eric Hansen's *Orchid Fever: A Horticultural Tale of Love, Lust, and Lunacy* (Hansen 2001). The Orchidaceae is the largest family of vascular plants in the world with an estimated 28,000 species and over 736 recognized genera (Chase et al. 2015; Christenhusz and Byng 2016). This vast diversity translates into a remarkable array of pollination mechanisms and growth forms, exemplifying the intricate adaptations of the orchid family. This is where Adam Karremans' book delves into the exploration of evolutionary adaptations for the reproductive success of orchids. Karremans' *Demystifying Orchid Pollination: Stories of Sex, Lies and Obsession* is an expertly curated dance that shows how to write good popular natural history while being deeply rooted in our current scientific understanding. There are 120 striking, well-placed, full-color photographs throughout the book that expertly illustrate the points discussed in the book and allow the reader to connect visually with the stories. The short, well-written forward by orchid specialist and author James Ackerman demonstrates well his deep understanding of orchids using clear language accessible to general audiences.

The book begins with an obligatory introduction to orchid morphology, natural history, and pollination syndromes, which also introduces Charles Darwin's fascination and extensive work with orchids. Darwin's pivotal role in the study of orchids and pollination is a recurring topic throughout the book. Readers without an understanding of orchid morphology can reference the nicely displayed floral parts of an orchid in Figure 1.2.2 on page 30 as they move through the book.

The author provides fascinating examples of deception where orchids lure pollinators through elaborate and devious ploys. The two main types of deception the author highlights are sexual and food deceptions. One example of sexual deception occurs in *Drakaea* (hammer orchids), in which the labellum of the flower mimics the appearance of flightless female thynnid wasps in order to attract males. The flower's hinged lip, disguised as a virgin female, lures the male wasp to it. As the male attempts to copulate with the orchid's lip, it slams the unsuspecting male wasp onto the column, ensuring pollen transfer before the frustrated male escapes hoping to find a less violent partner.

The focus then shifts to the fascinating ways orchids reward their pollinators beyond just nectar. These rewards include the orchids use of alluring fragrances, oils, and even the provision of convenient mating sites to attract the insects. For instance, *Maxillaria* flowers produce edible hair-like structures called trichomes that provide protein, oils, or starch for foraging insects. These trichomes have been colloquially referred to as "food-hairs."

Building upon this foundation, the book dives into the world of what Karremans identifies as "misfit" pollinators. These are animals beyond the usual suspects (bees, flies, wasps, birds, and butterflies) that have remarkably evolved partnerships with orchids. Examples of such evolutionary relationships with organisms are explored, including those with ants, beetles, aphids, and even some reptiles! Karremans dedicates a 15-page section to the natural history of the genus *Vanilla* (vanilla orchids), including a surprising revelation about its animal associates.

Some of the specialized morphological floral accessories are explained, showcasing the unique structures that have evolved to ensure successful pollination. The evolutionary toolkit employed by orchid flowers to ensure reproduction, which sometimes includes self-pollination and protandrous floral mechanisms is highlighted. Though the pace slows somewhat here, there are still enough exciting stories presented to keep the reader engaged.

Karremans dispels some of the common myths and misconceptions surrounding orchids, drawing a clear distinction between fact and fiction in both popular stories and scientific literature. He debunks misconceptions like the supposed orchid-mimicry hunting behavior of *Hymenopus coronutus* (orchid mantis) and the initial hypothesis that *Dendrophylax lindenii* (ghost orchid) was pollinated by *Cocytius antaeus* (giant sphinx moth) due to its long nectar spur. Overall, this discussion is a little more disjointed in its flow than other sections of the book, not only lacking some of the previous charisma, but also feeling a bit forced together. For example, the section "Somebody Told Me" tackles the misconception that all orchids rely on specific pollinators. However, the author clarifies that many orchid species are generalists that are able to attract a wider range of pollinators. This inclusion seems somewhat forced into the chapter.

The final chapter, "Change," delivers a sobering reminder of the ecological future facing many orchid species, including habitat destruction, orchid market exploitation, and climate change. One example of how climate change impacts orchids is the close relationship between the sexually deceptive *Ophrys sphegodes* (early spider orchid) and *Andrena nigroaenea* (solitary mining bee). The flower uses pseudocopulation as a pollination mechanism; however, as temperatures warm earlier in the year, the bee comes out of hibernation earlier before the orchid blooms. This phenological mismatch could lead to the orchid missing its chance of pollination altogether. Such disruptions in these essential synchronized life cycles pose a significant threat to the long-term survival of the orchid.

Throughout the book, Karremans uses QR codes to link the reader with videos associated with the narratives. These videos offer valuable opportunities to see the orchids and their unique features in action and add a unique experience for the reader, since the imagination may not be as proficient as seeing these interactions firsthand. However, the shift from paper-based reading to watching a video potentially leads the reader to high off-task distractions. This is exacerbated by the "recommended videos" from YouTube that appear after watching the intended video.

Overall, Karremans has done a spectacular job of connecting the reader with orchids in a digestible and educational way. As he notes in the first paragraph of the preface, "If wandering through these pages you are not astonished by the orchid's marvellous nature, I will have failed in my purpose." In this effort, he certainly did not fail. Karremans offers something for the experienced orchid specialist and the unexperienced layperson alike. As research unveils new stories, one should look forward to the sequel!

LITERATURE CITED

Chase, M. W., K. M. Cameron, J. V. Freudenstein, A. M. Pridgeon, G. Salazar, C. Chase, C. Van den Berg, and A. Schuiteman. (2015). An updated classification of Orchidaceae. Botanical Journal of the Linnean Society 177: 151–174.

Christenhusz, M. J. M., and J. W. Byng. (2016). The number of known plants species in the world and its annual increase. Phytotaxa 261: 201–217.

Hansen, E. (2001). Orchid fever: A horticultural tale of love, lust, and lunacy. Vintage Books, New York, N.Y.

Orlean, S. (1998). The orchid thief: A true story of beauty and obsession. Ballantine Books, New York, N.Y.

——Nathanael J. Pilla
Midwest Biological Survey, LLC
225 Michigan St.
Porter, Indiana, 46304
npilla@midwestbiologicalsurvey.com

ANNOUNCEMENT

ISOBEL DICKINSON MEMORIAL AWARD RECIPIENTS

Congratulations to **Krystal Sánchez** and **Josh G. Stepanek**, who are the recipients of the Isobel Dickinson Memorial Award for **best student-authored paper** published in *The Great Lakes Botanist*, Volume 60, 2021. The selected paper is entitled "Benthic Diatom (Bacillariophyta) Flora of Torch Lake, Michigan, an Oligotrophic, Alkaline Ecosystem with Evident benthic Diatom Production, with a Consideration of Some New and Interesting Species" by J.P. Kociolek, R.L. Lowe, K. Sánchez, and J.G. Stepanek, The Great Lakes Botanist 60: 24–55.

Congratulations to **Haley R. Weesies**, **Jonathan D. Walt**, **Zachary E. Hartwig**, and **Carolyn R. Koehn**, who are the recipients of the Isobel Dickinson Memorial Award for **best student-authored paper** published in *The Great Lakes Botanist*, Volume 61, 2022. The selected paper is entitled "Botanical Assessments of High-Quality Southern Shrub-Carr and Hardwood Swamp Wetlands in the Undeveloped Lowell Regional Greenspace, Kent County, Michigan" by Garrett E. Crow, David P. Warners, Haley R. Weesies, Jonathan D. Walt, Zachary E. Hartwig, and Carolyn R. Koehn, The Great Lakes Botanist 61: 2–34.

We acknowledge the Michigan Botanical Club—Dickinson Award Committee (Robert Ayotte, Bev Walters, Scott Warner, and Mike Penskar) for evaluation of the nominated student papers and the Michigan Botanical Society for funding this award.