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Exploring the influence of genetic diversity on pitcher plant restoration in Indiana Dunes National Lakeshore

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Figure 1. The northern pitcher plant traps prey in its tubelike pitcher structure where a suite of microorganisms digests prey and extracts nutrients needed for plant growth.

CARNIVOROUS PLANTS OBTAIN NUTRIENTS needed for growth through the breakdown of insects, microbes, and small amphibians. The most widely distributed carnivorous plant in North America is the northern pitcher plant (*Sarracenia purpurea* L., fig. 1), whose range stretches from northern Canada to the midwestern United States, and along the eastern U.S. coast south to the Gulf of Mexico. This species lives primarily in isolated, low-nutrient sphagnum moss bog and poor fen wetlands (fig. 2). Though individual populations are large, typically containing more than 100 plants, the species is in decline because of the loss of its specialized wetland habitat. The wetlands that host the northern pitcher plant are in a perilous position, often drained for development, mined for Sphagnum for the horticultural trade, or degraded by inputs of road salt and lawn and agricultural fertilizer runoff. Additionally, carnivorous plant enthusiasts prize this species and threaten population survival

through overcollection. As habitat and populations of the northern pitcher plant become increasingly rare, state and federal agencies are showing greater interest in conserving habitat and restoring plant populations.

Indiana Dunes National Lakeshore protects one of the few remaining populations of northern pitcher plant in the state (NatureServe 2007) (fig. 3). This population, located at the Indiana Dunes Pinhook Bog property, is isolated within an extensively developed landscape along the southern rim of Lake Michigan east of Gary, Indiana. Consequently, the national lakeshore has experienced declining populations of the northern pitcher plant. Scientifically informed management to restore this species is crucial to its survival in this and other fragmented ecosystems. Planning and implementing successful restoration of plant populations requires knowledge about how the plant functions ecologically,



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Figure 2. Though widespread in North America, the northern pitcher plant faces threats from loss and fragmentation of its specialized habitat: low-nutrient bog and poor fen wetlands. Indiana Dunes populations are genetically intermediate between the isolated island population of Isle Royale and the continuously interbreeding mainland populations of Apostle Islands and Pictured Rocks.

how it reproduces, what environmental qualities it requires, and how populations relate to each other genetically. Reestablishment of the pollination services provided by bees in Pinhook Bog will sustain the reproductive potential and genetic resilience of pitcher plants (Dixon 2009).

Importance of genetics in restoration planning

Sphagnum bog and fen wetlands south of Canada are typically isolated, separating populations of the northern pitcher plant both physically and by distance. This can lead to interesting conservation issues regarding the genetic relationships among different pitcher plant populations. One of the key questions ecologists have tried to answer is how fragmentation or isolation in the landscape affects genetic variation and gene flow of plant populations of a particular species. Wright (1969) developed the island model of migration among populations, which is frequently applied to landscape islands or fragmented natural areas such as the habitat of the northern pitcher plant. He hypothesized that within populations of a species, two important genetic forces function between isolated or island populations: (1) gene flow originating from outside populations that maintain genetic relatedness between populations either through pollen or seed exchange, and (2) genetic drift occurring within populations that create more genetically different subpopulations (Allendorf and Luikart 2007). The more geographically isolated a population becomes, the less gene flow will occur between populations, increasing genetic drift and potentially creating genetically distinct populations (Kimura and Weiss 1964; Allendorf and Luikart 2007). Essentially, the amount of divergence between two populations is a balance between gene flow homogenizing the populations and genetic drift differentiating the populations. The more isolated the populations, the less balanced these processes are, thus leading to increased genetic divergence.

Effects of genetic isolation within populations complicate habitat and plant species restoration planning. Isolated populations experiencing genetic drift and increased inbreeding can become locally adapted to a particular site (Hufford and Mazer

2003; Allendorf and Luikart 2007). Using seed or plants from distant populations that are planted with locally adapted populations to restore new sites could lead to reduced fitness in offspring from crosses between the locally adapted and distant populations in the restoration site (Hufford and Mazer 2003). Careful consideration and understanding of the genetic relatedness of populations become important in restoration when considering supplementing plant populations with outside seed sources.

Consider these two examples of how genetic understanding can aid ecosystem management:

- Imagine many populations of a plant species where pollen and seeds are continually being exchanged among the populations. These pollen and seeds represent gene flow among the populations, and the more gene flow that occurs, the more similar the populations become to each other genetically. Where some event has reduced, destroyed, or removed a plant population from a site, managers can potentially restore the population by collecting and reintroducing

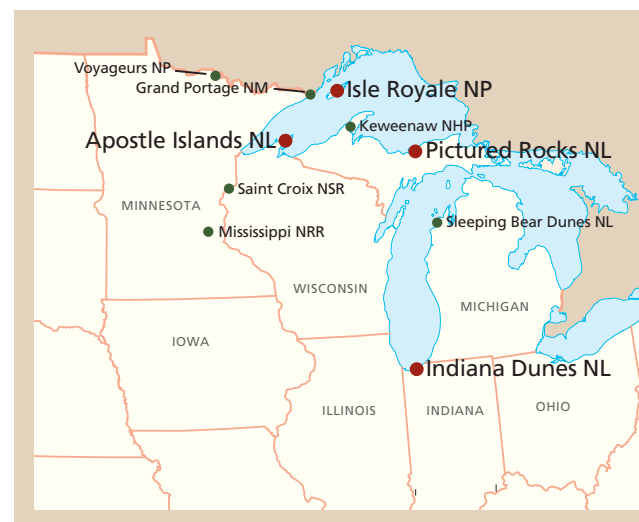


Figure 3. This study assessed the population genetics of pitcher plants in four national park units of the Great Lakes region shown by the red dots: Isle Royale National Park and Indiana Dunes, Pictured Rocks, and Apostle Islands national lakeshores. The main goal of the study was to determine if abundant populations of pitcher plants in some parks could be used to supplement decreasing populations at Indiana Dunes National Lakeshore without compromising local population genetics or reducing successful local adaptations.

The amount of divergence between two populations is a balance between gene flow homogenizing the populations and genetic drift differentiating the populations.

seeds from any of the surrounding populations because all of the populations are genetically similar. Consideration of restoration sites may thus focus on those with similar ecological conditions, rather than the genetic component.

- In the second scenario, many populations of a plant species are still spread across the landscape, but one population is isolated on an island in a lake. This population is so isolated by distance from other populations that very little seed or pollen exchange occurs between the island and the mainland; therefore, gene flow is very low for this population. As gene flow is reduced, populations can begin to become genetically different from each other, and this is an illustration of genetic drift. If the island population requires reintroduction, managers need to carefully consider where to select seeds to restore this population. Introducing seed from outside sources could lead to the loss of the local plants' genetic uniqueness, and potentially decrease the success of restoration attempts.

Fortunately, populations of northern pitcher plant are still fairly abundant in other national park units within the western Great Lakes region. We wished to assess whether some of these populations could serve as potential seed sources for restoration of this plant species within Indiana Dunes National Lakeshore. The northern pitcher plant has continuously exhibited low genetic diversity within and among populations throughout the eastern United States (Godt and Hamrick 1996; Schnell 2002; Karberg and Gale 2006). This means that throughout its range the plant has consistently displayed low genetic differences between individuals and between populations regardless of distance between populations. This would indicate that most populations are genetically similar and seed sources for restoration could be plentiful.

We wished to examine differences in genetic variation between the Pinhook Bog population located within Indiana Dunes National Lakeshore and three other national park units in the western Great Lakes area—Isle Royale National Park (Michigan), Apostle Islands National Lakeshore (Wisconsin), and Pictured Rocks National Lakeshore (Michigan)—to determine the possibility of using seed from regional sources for restoration at Indiana Dunes (see fig. 3).

Genetic analysis of the western Great Lakes populations

We collected plant leaves for molecular genetic analysis to determine the genetic relatedness of populations at each of the four sampled national parks: Apostle Islands, Indiana Dunes, Isle Royale, and Pictured Rocks. The analysis indicated a strong degree of clonal growth, created by asexual reproduction, evidenced by moderate within-population genetic diversity (Nei's gene diversity = 0.3770 ± 0.1289). Clonal species tend to have lower overall genetic diversity within a population because of their nonsexual reproductive methods. The northern pitcher plant has often been hypothesized as being clonal (Schwaegerle and Schaal 1979). This moderate amount of genetic diversity was examined using an analysis of molecular variance (AMOVA) to see how much variation exists within individual populations and how much exists between or among populations at different locations. The total variation explained by genetic differences between populations located in each park ($F_{ST} = 0.2688$, $p < 0.0001$) indicates that 26.88% of the observed genetic diversity was accounted for by population variation. In essence, our sampled populations are 26.88% genetically different from each other. To determine what this means in terms of how the individual populations are related to each other, a visual analysis of the genetic dissimilarity of populations is necessary. Genetic distance or genetic dissimilarity of populations can be graphically represented with a dendrogram or diagram tree that illustrates how closely related populations are genetically. An examination of the visual patterns of genetic distance between populations revealed genetic differences that distinguished Indiana Dunes and Isle Royale populations from the other two parks (fig. 4). This dendrogram graphically represents genetic distance between individual populations and illustrates that Isle Royale populations, segregated on a separate branch of the dendrogram, have the greatest genetic distance from the other park populations. Apostle Islands and Pictured Rocks populations are closely intermixed and not well separated by genetic distance. Indiana Dunes populations are genetically intermediate between the isolated island population of Isle Royale and the continuously interbreeding mainland populations of Apostle Islands and Pictured Rocks.

Natural and landscape island populations

The two populations of the northern pitcher plant that exhibited the most genetic differentiation from the other populations are both fairly isolated populations: the natural island population of Isle Royale National Park is isolated within Lake Superior, and the landscape island population of Indiana Dunes National Lakeshore is isolated within a highly human-altered, fragmented landscape. The genetic differentiation of these two populations as compared to mainland populations found in a non-fragmented landscape can potentially be explained by habitat isolation. The natural island population (Isle Royale) is located on an isolated island within Lake Superior that has lacked a physical connection to the mainland since the last glaciation (Dorr and Eschman 1970; Huber 1983). Northern pitcher plant seeds are not believed to be consumed by birds or mammals, which would facilitate distribution over water, but rather typically disperse close to the parent plant (Ellison and Parker 2002). The barrier of large stretches of open water may likely be the reason for genetic differentiation of the northern pitcher plant populations on Isle Royale since the water barrier reduces the possibility of gene flow

and increases population inbreeding and genetic drift, making the population more genetically distinct from mainland populations.

In evaluating the results of our genetic analysis, which differentiated the landscape island population of Indiana Dunes from other intact populations, we think that larger expanses of fragmented landscape may also provide a sufficient barrier, reducing gene flow to the Indiana Dunes population. The two nearest populations of the northern pitcher plant to Indiana Dunes are located 45 miles (73 km) and 96 miles (154 km) away from the study site (NatureServe 2007). Hypothetically, 45 miles (73 km) of fragmented landscape may represent the outer bounds of a fragmentation threshold for this plant, beyond which genetic differentiation among populations increases as gene flow proportionally decreases.

The mechanism for genetic differentiation of the landscape island population may be related to gene flow and distance, with Indiana Dunes receiving little gene flow from outside populations because of distance, thus increasing the action of genetic drift. Pollinators of the northern pitcher plant include two bee species, *Bombus affinis* and *Augochlorella aurata*, and one fly species, *Flecherimyia fletcheri* (Ne'eman et al. 2006). Observations suggest that specific pollinators are limited at the Indiana Dunes site (A. Molumby, University of Illinois–Chicago, personal observation). Research has shown that wild bee pollinations are limited by habitat isolation; increased distance from suitable habitat leads to decreased bee visitations (Steffan-Dewenter and Tscharnkte 1999). This factor of limited pollen dispersal contributes to the landscape isolation of populations within both of the sampled “island” populations.

Indiana Dunes northern pitcher plant populations show a degree of genetic isolation from other national park populations. This is a plant species that has historically shown a low degree of genetic variation, so even small amounts of genetic differentiation could be significant. Understanding how populations with this degree of isolation would respond to restoration through introduction of outside seed sources or plants is not yet fully understood. The accepted general standard among restoration ecologists is to utilize seeds or vegetative plant material

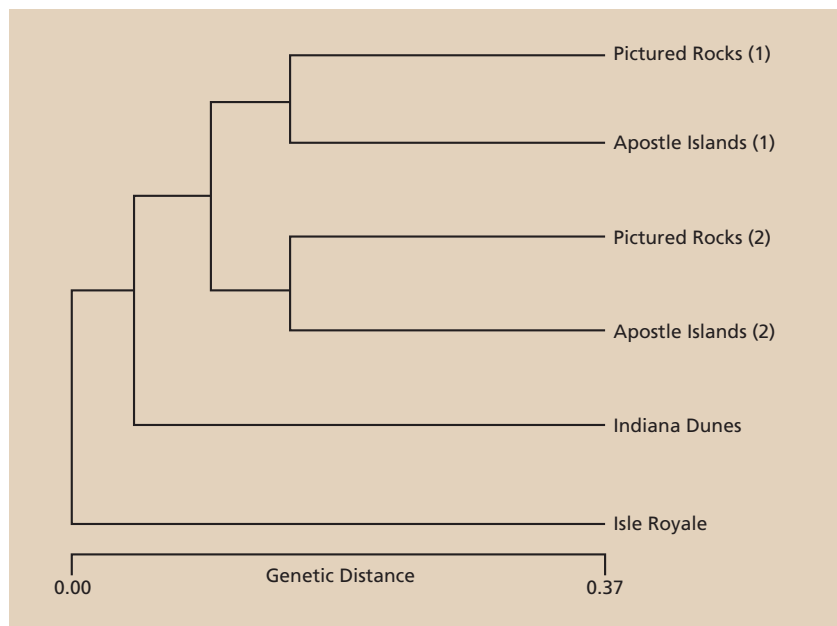


Figure 4. This dendrogram illustrates the genetic distance between the six sampled populations of northern pitcher plant. The Isle Royale and Indiana Dunes branches are separated from the other two parks, indicating unique genetic patterns in these populations. The more distant or separate the branch, the more genetically distant the populations.

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Figure 5. Investigators are growing pitcher plants from seed in greenhouse conditions at Indiana Dunes for wetland restoration. These seedlings take 3 to 5 years to reach maturity, which may not be desirable for restoration plans.

collected within a 50-square-mile (12,950 hectares) area immediately surrounding the restoration site. However, this generalization is anecdotal and needs to be examined scientifically, given what we have learned about clonality and genetic differentiation due to geographical isolation in the northern pitcher plant. To examine restoration possibilities at Indiana Dunes, a common garden experiment could be undertaken to examine responses of plants and seeds from all four national parks planted side by side in a single site (fig. 5). Examining the growth responses and interbreeding fitness of plants from these different populations on one substrate type would help determine whether observed genetic differences are ecologically significant.

Lessons for restoration

The northern pitcher plant has historically exhibited low genetic variability, with populations very genetically similar to each other often across great distances. However, this study did document appreciable genetic differentiation between isolated, island populations and mainland populations. Currently, northern pitcher plant populations in Indiana Dunes show some genetic distinction from other mainland populations. Genetic isolation caused by artificial geographic barriers, such as urban and agricultural development, limits cross-pollination and thus possibly reduces genetic variation in the Pinhook Bog population. A decrease in pollinator populations may also be contributing to limited gene flow. Previous researchers have noted that the habitat for bumblebees, the natural pollinators of the pitcher plant, is lacking in Pinhook Bog (A. Molumby, University of Illinois–Chicago, personal communication). Another factor contributing to decline of the pitcher plant populations is the expansion of highbush blueberries (*Vaccinium corymbosum*) in the bog. The pitcher plant is shade-intolerant and thus plant growth is limited because of shading effects of blueberry plants. (Mystery surrounds the origin of blueberry plants in Pinhook Bog. Anecdotal evidence suggests that a previous property owner planted them for agriculture prior to authorization of the national lakeshore in 1966.) The major question is: Is this amount of genetic differentiation or genetic identity observed in the Indiana Dunes populations enough to preclude the use

of outside seed sources for restoration of declined northern pitcher plant populations? This study alone is not enough to conclusively predict the results of introducing outside genetic sources but the differences are large enough to argue for caution and further exploration before using outside sources. The northern pitcher plant has consistently shown smaller amounts of genetic diversity across its range. It's a clonal plant, which typically reduces genetic diversity within a species, and yet significant differences were still detected between Indiana Dunes populations and populations in other parks. Before outside introduction, a common garden study should be conducted to determine the influence of local genetics versus local environment on northern pitcher plant ecology.

In the meantime, what are the options to restore pitcher plant populations in Indiana Dunes National Lakeshore? One is to improve habitat conditions for pitcher plant establishment. Managers have begun removing blueberry plants to create more open habitat suitable to the northern pitcher plant. To hasten restoration at Pinhook Bog, managers can attempt to increase seed set through hand pollination, promoting local seed production. Transplanting vegetative clones can also be conducted within the bog. Introduction of associated bee pollinators and their required habitat is also recommended. Indiana Dunes pitcher plant populations do show some degree of genetic isolation from the other national park populations, and the consequences of using outside plants and seeds to supplement restoration efforts are questionable. More research, especially using common garden experiments, is needed to determine if introduced plants from other regions of the Great Lakes can successfully reproduce without reducing the genetic integrity of northern pitcher plant populations in Indiana Dunes. The results from plants grown from clones would be faster than from seed-derived plants, which would not be available for 3 to 5 years, given the slow maturation from seed establishment to adult plants of this species (fig. 5). In the meantime, increasing habitat quality and facilitating seed set of native populations may be the best way to restore pitcher plant populations today at Indiana Dunes.

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For further information

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