

Asplenium bradleyi

Bradley's Spleenwort

Aspleniaceae



Asplenium bradleyi courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

***Asplenium bradleyi* Rare Plant Profile**

New Jersey Department of Environmental Protection
State Parks, Forests & Historic Sites
State Forest Fire Service & Forestry
Office of Natural Lands Management
New Jersey Natural Heritage Program

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Life History

Asplenium bradleyi (Bradley's Spleenwort) is a small fern in the Aspleniaceae. A number of the *Asplenium* species in the eastern United States are very closely related and have similar life histories and somewhat overlapping morphological characteristics. Wagner (1954) outlined the relationships within the group, identifying three 'basic' species from which the others were derived: *A. montanum* (Mountain Spleenwort), *A. platyneuron* (Ebony Spleenwort), and *A. rhizophyllum* (Walking Fern). Wagner's proposal that *Asplenium bradleyi* initially arose as a fertile hybrid of *A. montanum* and *A. platyneuron* was subsequently confirmed by a genetic analysis (Werth et al. 1985). Crosses of *A. montanum* and *A. platyneuron* have also been known to produce sterile hybrids (Wagner et al. 1973), and Werth et al. (1985) suggested that *A. bradleyi* may have arisen more than once.

The life cycle of ferns includes two independent generations. Spores produced by mature plants initially develop into tiny free-living gametophytes with structures that produce male and female reproductive cells (gametes). Male gametes (sperm) develop in an antheridium and a female gamete (egg) develops in an archegonium. Fertilized female cells develop into the leafy plants (sporophytes) that produce the spores for the next generation, and once the sporophytes are large enough to be self-sufficient the gametophytes disintegrate (Raven et al. 1986). Apogamy—the development of a sporophyte from a gametophyte without fertilization—has been reported in some species (e.g. *Asplenium unilaterale*) but is not common in the spleenwort family (Nayar and Kaur 1971).

Gametophytes of ferns in the Aspleniaceae establish on top of the substrate. The tiny plants are flat, somewhat heart-shaped, and green with a lighter-colored midrib. In some spleenworts they are hairy (Nayar and Kaur 1971, Wagner et al. 2020). Knowledge regarding the gametophyte stage is lacking for many ferns (Farrar 1976) but that generation appears to be comparable among the *Asplenium* species that have been studied. The development of *Asplenium platyneuron*, one of the parent species of *A. bradleyi*, was observed by Pickett (1914a). By the time *A. platyneuron* gametophytes were ten weeks old they usually had mature reproductive organs and were capable of developing sporophytes. However, a significant number of plants wintered over in the gametophyte generation and produced sporophytes during the following season.

Asplenium bradleyi sporophytes are perennial from a short rootstock and the bases of old stalks can often be seen among the current fronds. The fronds are 5–20 cm long. The leaf petiole (or stipe) is chestnut brown and the brown color continues into the lower part of the rachis (stem portion in the center of the blade), changing to green in the upper half or third of the blade. The oblong, lance-shaped leaves are mostly divided into alternating pinnae that are short-stalked and distinctly lobed but the uppermost part of each leaf is simply lobed. The outer ends of the lobes are slightly toothed and the clusters of sporangia (sori) are linear and straight or slightly curved. (See Eaton 1873, Britton and Brown 1913, Fernald 1950, Gleason and Cronquist 1991, Montgomery and Fairbrothers 1992, Wagner et al. 2020). Both the sterile and fertile fronds of *A. bradleyi* are evergreen (Wherry 1957). One of its parent species, *A. montanum*, is also considered evergreen but the leaves can sometime become discolored or desiccated so that the plants appear brown until new fronds emerge the following spring (NYNHP 2022a). The leaves

of *A. bradleyi* are often spreading (Gleason and Cronquist 1991), and Lee (1909) observed that the ferns "spread their leaves against the face of the rocks like little stars or rosettes." A dwarf form of *A. bradleyi* was documented by Weber and Mohlenbrock (1958) who found plants with reproductive fronds 1.2–3 cm in length, some of which also lacked rachis pigmentation, growing with more typical plants.



Left: Britton and Brown 1913, courtesy USDA NRCS 2022a. Right: Jim Keesling, 2016.

Asplenium bradleyi has been known to hybridize with several other spleenworts, including both of its parent species, although the hybrid that results from crosses with *A. platyneuron* is relatively unknown (Wherry 1925) and has not been named. All of the hybrids are typically sterile (Wagner et al. 2020). The uncommon hybrid of *A. bradleyi* and *A. montanum* (*Asplenium* × *wherryi*) was first collected in New Jersey (Smith et al. 1961), where it has been documented in two counties. *A.* × *wherryi* is similar in appearance to *A. bradleyi* but is distinguishable by its aborted spores (Montgomery and Fairbrothers 1992). The hybrid of *A. bradleyi* and *A. pinnatifidum* (*Asplenium* × *gravesii*) is more widely distributed (Kartesz 2015) and at least some occurrences may be self-perpetuating (Wherry 1925). *A.* × *gravesii* has not been documented in New Jersey, and its parent species have not been found growing together in the state (NJNHP 2022). Even where the parent plants do co-occur the hybrid is not common (Darling 1957).

Pollinator Dynamics

Because *Asplenium bradleyi* is a non-flowering plant, pollination does not take place. Antheridia on the gametophytes release their gametes through a pore-like opening that develops in the cap cell (Nayar and Kaur 1971). Fertilization is dependent on water, which allows the movement of the multiflagellate sperm toward a receptive egg cell (Raven 1986).

Some pteridophytes can manipulate the sequence of gamete development in order to promote cross-fertilization, but it is not certain whether this occurs in *Asplenium bradleyi*. The Hart's-

tongue Fern (*Asplenium scolopendrium*) utilizes a mixed mating system, outcrossing when circumstances permit but self-fertilizing when necessary. The latter strategy permits the colonization of a new site by a single spore (Wubs et al. 2010). Genetic variability is low in young colonies of *A. ruta-muraria* but it increases as the populations age (Schneller and Holderegger 1996). The authors suggested that for *A. ruta-muraria* and similar species that occur in small, isolated colonies genetic variation is probably less important to the maintenance of populations than ecological and demographic factors.

Seed Dispersal

Dispersal in *Asplenium bradleyi* is carried out by spores rather than seeds. Bradley's Spleenwort develops 64 spores in each sporangium (Wagner et al. 2020). The dust-like spores are dispersed by wind and can fall within a few meters of the parent plant or be carried for great distances (Kessler 2010). In New Jersey, mature spores of *A. bradleyi* may be present from July to September but primarily mature in September (Hough 1983). Many ferns disperse their spores slowly over a long period, sometimes continuing into the following spring (Farrar 1976) and that has been observed in several kinds of *Asplenium* (Pickett 1914b). Darling (1957) successfully germinated *A. bradleyi* spores that were collected from wild plants during January.

The early development of *Asplenium bradleyi* has not been well-documented but the process has been described for a number of other *Asplenium* species and it appears to be fairly consistent within the genus. On suitable substrate, the spores of *A. platyneuron* usually germinate over a period that may last for several weeks (Pickett 1914a). Pickett observed that the staggered release times and germination periods of *Asplenium* spores can reduce potential losses from severe conditions such as freezing or drought. When conditions are favorable the spores absorb water and swell to twice their size and then rupture to release their contents (Pickett 1914b). Morlang (1967) reported that an unidentified type of bacteria facilitated germination in three related ferns: *A. rhizophyllum*, *A. montanum*, and *A. platyneuron*. Germination of *Asplenium* spores initially produces a rhizoid and a filament 4–8 cells long and one cell wide (Nayar and Kaur 1971, Testo and Watkins 2011). In *A. platyneuron*, early development is highly influenced by light availability and in certain conditions the gametophytes can reproduce vegetatively (Pickett 1914a).

Asplenium spores sown in laboratories typically germinated in 5–28 days (Pickett 1914a and 1914b, Herraro et al. 1993, Pangua et al. 1994, Testo and Watkins 2011). Longer germination times have been reported in shade (Pickett 1914b) and at lower temperatures (Pangua et al. 1994). In comparison to an average germination period of 1–3 weeks under laboratory conditions germination in the field took longer, with gametophytes appearing after 4–8 weeks for *A. trichomanes* and 8–12 weeks for *A. ruta-muraria* (Pangua et al. 1994). Archegonia and antheridia were present six weeks after germination (Pickett 1914b, Herraro et al. 1993), at which point the average size of gametophytes was ~0.5 mm² (Pangua et al. 1994). *Asplenium* gametophytes can be bisexual, exclusively male, or exclusively female, and Pangua and her colleagues noted that fully developed gametophytes with archegonia were always the largest (6–10 mm²) while those with only antheridia typically reached maximum sizes of 1–2 mm². As previously noted, sporophyte development may proceed rapidly or the ferns may remain in the

gametophyte stage for several months depending on environmental conditions (Pickett 1914a, 1914b).

Mycorrhizal associations have not been reported for *Asplenium bradleyi*. Development of mycorrhizae is highly variable in the genus, and approximately half of the species in Aspleniaceae are non-mycorrhizal (Wang and Qiu 2006). Ferns that inhabit isolated rock outcroppings and crevices often lack mycorrhizae (Berch and Kendrick 1982).

Habitat

Asplenium bradleyi can be found at elevations up to 1000 meters on rocky outcrops and cliffs where it may establish on open ledges or grow in sheltered microsites within crevices or beneath shelves (Lee 1909, Pretz 1911, Tuttle 1915, Lyle 1980, Homoya et al. 1985, Rhoads and Block 2007, Wagner et al. 2020, NYNHP 2022b). The species has occasionally been observed growing on boulders that have fallen from cliffs (Williamson 1878, Wherry 1928). Ostlie and Treher (2018) noted that few other vascular plants are able to flourish in the small spaces and harsh environment occupied by *A. bradleyi*. Anderson (1931) described one *Asplenium bradleyi* microsite as "a damp, cold perpendicular rift which no sunshine could enter" although it seems likely that the plants received light for at least some portion of the day. The fern's habitat is frequently described as dry and at least partially shaded (Williamson 1878, Harvey 1880, Lee 1909, Rhoads and Block 2007, Ostlie and Treher 2018).

Throughout its range Bradley's Spleenwort is most often associated with sandstone, but the species has also been reported as growing on chert, gneiss, granite, schist, quartzite, and metaquartzite (Williamson 1878, Harvey 1880, Lee 1909, Wherry 1920, Campbell 1921, Anderson 1931, Mohlenbrock and Engh 1964, Peck 2011, Weakley 2015, Ostlie and Treher 2018). The soils derived from the substrate are generally acidic (Wherry 1920, 1928, 1931; Fairbrothers and Hough 1973, Montgomery 1982, Rhoads and Block 2007, Wagner et al. 2020, NYNHP 2022b). One early document erroneously reported *A. bradleyi* on limestone and was subsequently copied by other authors, but Wherry (1920) established the species' preference for mediacid to subacid soils and repeatedly published corrections (e.g. Wherry 1928, 1931) until the record was rectified (Wagner 1983). Wherry (1920) observed that the soil requirements of *A. bradleyi* were essentially identical to those of *A. montanum*. However, Marchant et al. (2016) found that Bradley's Spleenwort occupies an abiotic niche intermediate to those of *A. montanum* and *A. platyneuron*, thereby avoiding direct competition with its parent species.

Wetland Indicator Status

Asplenium bradleyi is not included on the National Wetlands Plant List (NWPL). Any species not on the NWPL is considered to be Upland (UPL) in all regions where it occurs. The UPL designation means that it almost never occurs in wetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2022b)

ASBR2

Coefficient of Conservatism (Walz et al. 2018)

CoC = 8. Criteria for a value of 6 to 8: Native with a narrow range of ecological tolerances and typically associated with a stable community (Faber-Langendoen 2018).

Distribution and Range

The worldwide range of *Asplenium bradleyi* is limited to the central and eastern United States (POWO 2022). The map in Figure 1 depicts the extent of Bradley's Spleenwort in North America.

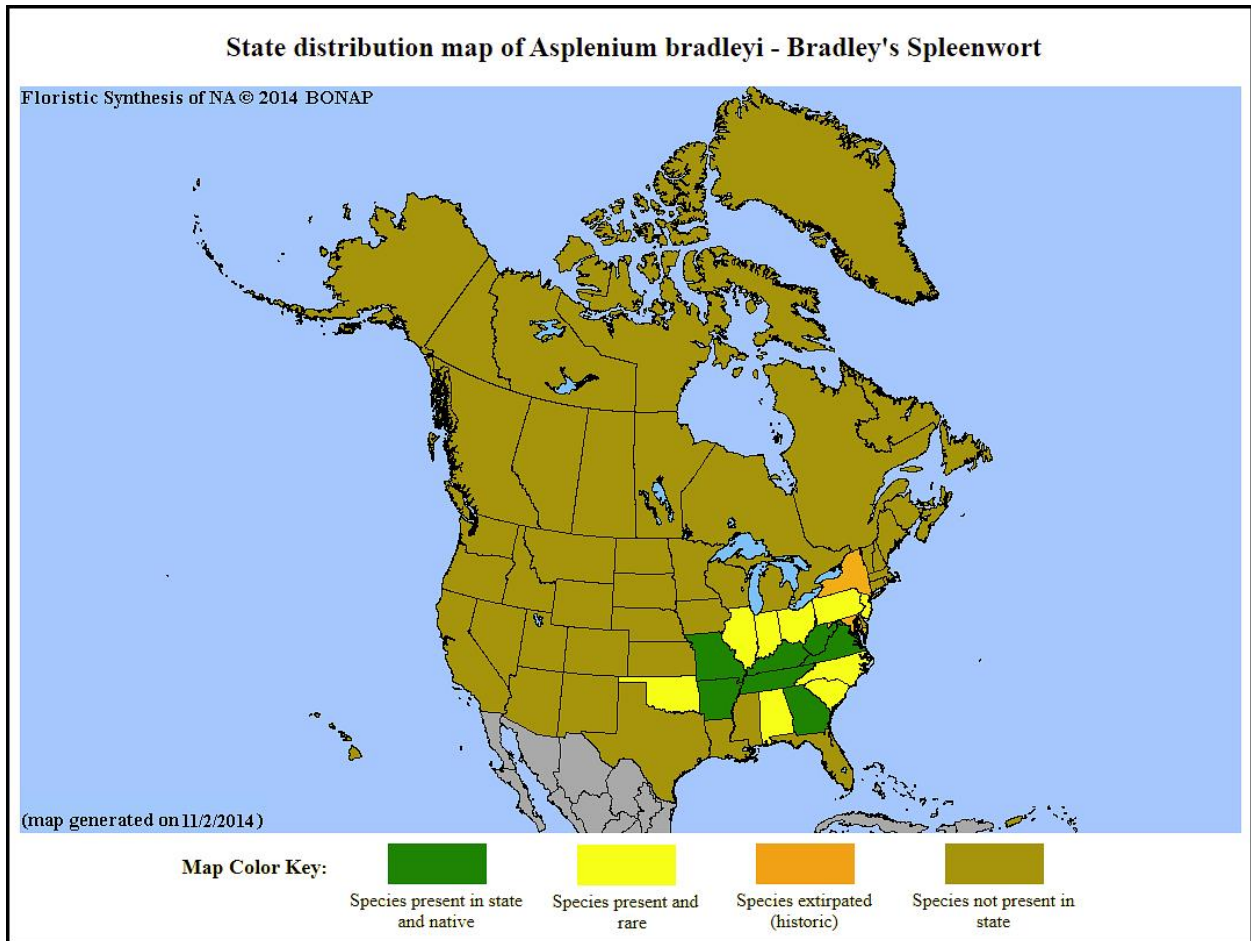


Figure 1. Distribution of *A. bradleyi* in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2022b) shows records of *Asplenium bradleyi* in two New Jersey counties: Morris and Warren (Figure 2 below). Bradley's Spleenwort was also historically known from Passaic County (Fairbrothers and Hough 1973, Mid-Atlantic Herbaria 2022).

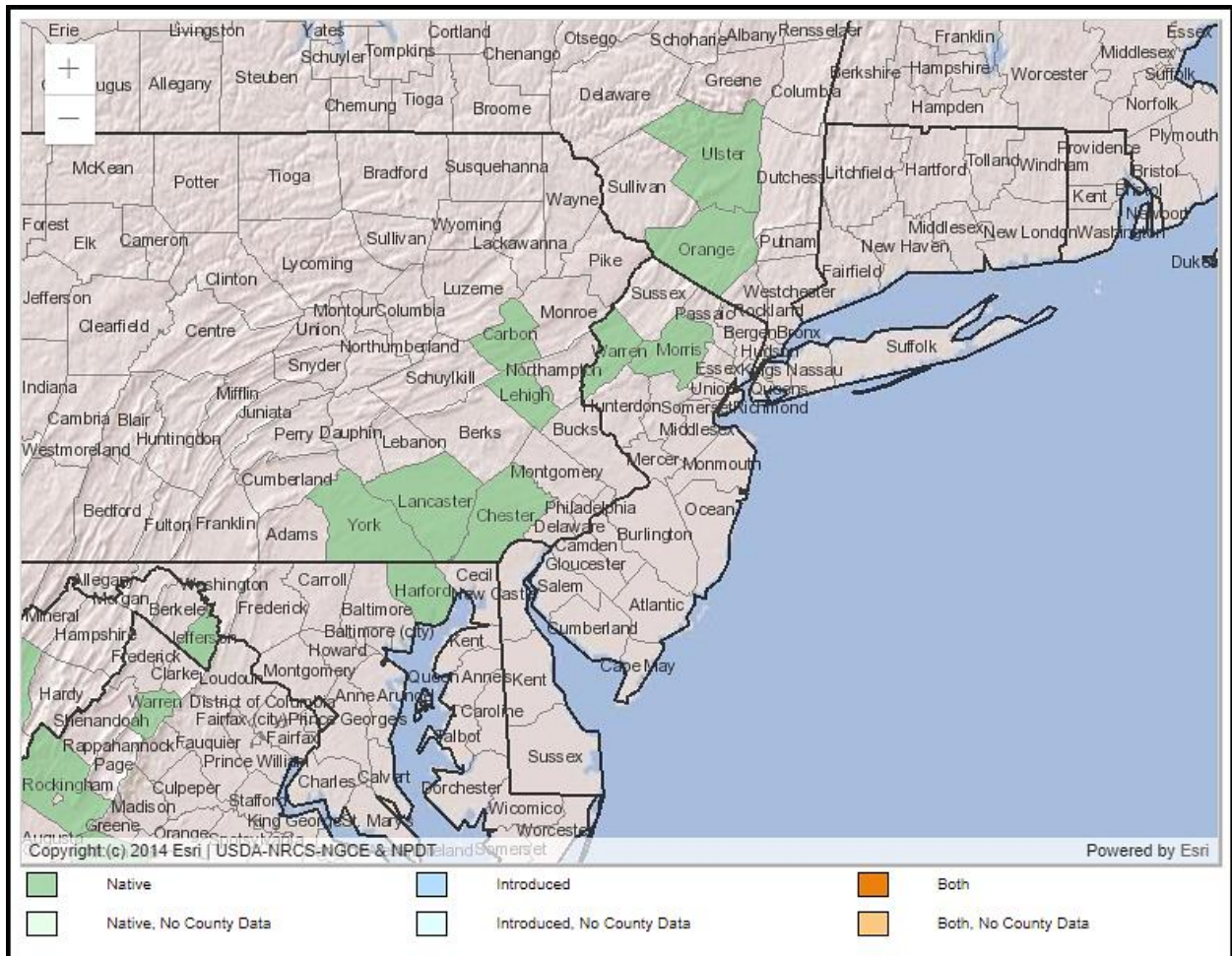


Figure 2. County records of *A. bradleyi* in New Jersey and vicinity (USDA NRCS 2022b).

Conservation Status

Asplenium bradleyi is apparently secure at a global scale. The G4 rank means the species is at fairly low risk of extinction or collapse due to an extensive range and/or many populations or occurrences, although there is some cause for concern as a result of recent local declines, threats, or other factors (NatureServe 2022). In North America, *A. bradleyi* has also been identified as a plant species of highest conservation priority for the North Atlantic region, which includes four Canadian provinces and twelve U. S. states. The species has a regional rank of R2 (imperiled), signifying a high risk of extinction (Frances 2017).

The map below (Figure 3) illustrates the conservation status of *Asplenium bradleyi* throughout its range. Bradley's Spleenwort is critically imperiled (very high risk of extinction) in nine states, imperiled (high risk of extinction) in five states, vulnerable (moderate risk of extinction) in one

state, and possibly extirpated in New York. The species has not been ranked in three additional states where it has been recorded.

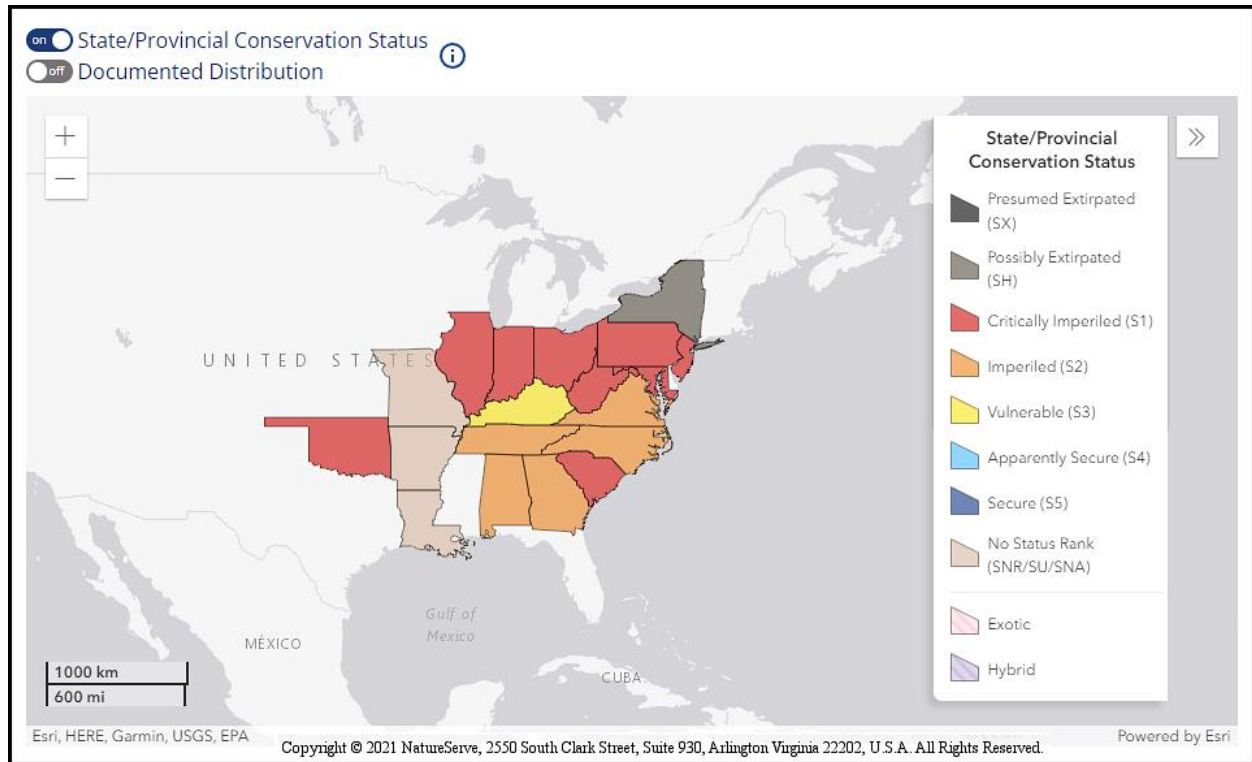


Figure 3. Conservation status of *A. bradleyi* in North America (NatureServe 2022).

New Jersey is one of the states where *Asplenium bradleyi* is critically imperiled (NJNHP 2022). The S1 rank signifies five or fewer occurrences in the state. A species with an S1 rank is typically either restricted to specialized habitats, geographically limited to a small area of the state, or significantly reduced in number from its previous status. *A. bradleyi* is also listed as an endangered species (E) in New Jersey, meaning that without intervention it has a high likelihood of extinction in the state. Although the presence of endangered flora may restrict development in certain communities, being listed does not currently provide broad statewide protection for plants. Additional regional status codes assigned to the plant signify that the species is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Asplenium bradleyi has always been rare in New Jersey (Montgomery 1982). The species was first documented in New Jersey early in 1935 with the discovery of a single plant, but a subsequent visit to the site later turned up several additional plants (Wherry 1935). The original occurrence was relocated by Vincent Abraityis in 1960 after the site was thought to have been destroyed (Snyder 1984) and it is one of two locations where Bradley's Spleenwort is presently considered to be extant in the state (NJNHP 2022).

Threats

No imminent threats have been identified for extant populations of *Asplenium bradleyi* in New Jersey (NJNHP 2022) although one of the occurrences was once noted as potentially vulnerable to overcollection or development (Fairbrothers and Hough 1973). Overcollection has long been cited as a threat to *A. bradleyi* (Waters 1920, Hill 2003, NYNHP 2022b) and it was identified as the cause of extirpation for at least one population (Darling 1957).

Throughout its range, a number of other anthropogenic threats may put *Asplenium bradleyi* populations at risk. Habitat destruction related to resource extraction has been identified as a primary concern, particularly relative to strip-mining activities and certain logging practices (Tompkins 2018, Ostlie and Treher 2018, PANHP 2019). Ostlie and Treher (2018) also cited the extirpation of a population that had been adjacent to a road, although the specific cause of the loss had not been ascertained. It is likely that contamination from the application of road salts, herbicides, or fertilizers in developed areas situated uphill from cliffside occurrences would have a harmful effect on the ferns. Remote locations on steep terrain may protect many *A. bradleyi* occurrences from direct disturbance but in some settings recreational rock-climbing can become a problem. One Ohio population was nearly destroyed in that manner (Ostlie and Treher 2018). Minicuci (2019) identified the activity as a potential threat to *Asplenium montanum*—which has similar life history characteristics and habitat preferences—noting that climbers could directly damage extant plants, inadvertently introduce invasive species, or alter the chemistry of ledges by depositing chalk.

Lyle (1980) observed that *Asplenium bradleyi* exemplified species for which landscape features can prohibit their widespread occurrence. Proliferation of *A. bradleyi* is naturally limited by the interaction of its life history characteristics (e.g. random spore dispersal) and narrow habitat requirements. The success of the spleenwort may also be influenced by climatic conditions. A study of one of its parent species, *A. platyneuron*, found that while the gametophytes were able to withstand exposure to winter temperatures as low as -23 °C and survive extended periods of desiccation, a summer drought reduced spore production and caused mortality in the sporophytes (Pickett 1914a). Drought has also been implicated in the losses of *A. bradleyi* plants and even whole colonies (Lee 1911, Darling 1957, Ostlie and Treher 2018). As climate change ushers in an era of rising temperatures and extended droughts it is likely to have negative consequences for Bradley's Spleenwort.

Management Summary and Recommendations

The distribution of *Asplenium bradleyi* is limited by its narrow habitat requirements, so conservation of both extant populations and suitable habitat in their vicinity is a priority for the species. In certain locations, habitat protection may require an additional buffer area in order to maintain tree cover or limit uphill development and the associated runoff. At sites where the fern could be harmed by recreational activities, trails or climbing routes should be redirected to avoid damage to the plants. Occurrences should be monitored periodically for emerging threats from disturbance or invasive species. Populations of *Asplenium bradleyi* are often limited to small numbers of plants growing in inaccessible locations so it is difficult to search for new

occurrences. However, in cases where potential habitat is likely to be impacted by development or resource extraction searches for the species should be prioritized.

Studies of other *Asplenium* species have created a solid foundation for understanding the patterns of establishment and development in the genus. However, the investigations have also highlighted some differences within the group, underscoring the importance of species-specific research for the development of meaningful management strategies. In his quest to learn about the hybrid *A. gravesii*, Darling (1957) raised both *A. bradleyi* and *A. pinnatifidum* from spores (and yes, he also got a few hybrids). While his experience provided some information about the growth of *A. bradleyi* in a controlled situation, research conducted in natural settings could impart useful knowledge concerning the ways in which microhabitat characteristics and climatic conditions influence the fern's reproductive success. A native plant gardening guide by Leopold (2005) indicated that *A. bradleyi* is well-suited for shaded rock gardens but provided no information regarding propagation. In addition to a better understanding of *A. bradleyi*'s developmental needs, it would also be helpful to know what limits the spleenwort to such seemingly inhospitable habitat and whether the species is self-compatible and able to establish from a single spore.

Synonyms

The accepted botanical name of the species is *Asplenium bradleyi* D. C. Eaton. Orthographic variants, synonyms, and common names are listed below (ITIS 2022, POWO 2022, USDA NRCS 2022b).

Botanical Synonyms

Asplenium pinnatifidum var. *stotleri* (Wherry) Clute
Asplenium stotleri Wherry
Asplenium × *stotleri* Wherry (pro sp.)
Chamaefilix bradleyi Farw.

Common Names

Bradley's Spleenwort

References

Anderson, W. A. Jr. 1931. A list of Tennessee ferns. *American Fern Journal* 21(1): 11–20.

Berch, Shannon M. and Bryce Kendrick. 1982. Vesicular-arbuscular mycorrhizae of southern Ontario ferns and fern-allies. *Mycologia* 74(5): 769–776.

Britton, N. L. and A. Brown. 1913. *An Illustrated Flora of the Northern United States and Canada in three volumes: Volume I (Ferns to Buckwheat)*. Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 680 pp.

Campbell, Elmer Grant. 1921. Some aspects of Stone Mountain and its vegetation. *Proceedings of Indiana Academy of Science* 31: 91–100.

Cressler, Alan. 2011. Cover photo of *Asplenium bradleyi*. Courtesy of the Lady Bird Johnson Wildflower Center, <https://www.wildflower.org/>. Used with permission.

Darling, Thomas Jr. 1957. In search of the rock-fern hybrid *Asplenium gravesii*. *American Fern Journal* 47(2): 55–66.

Eaton, D. C. 1873. New or little-known ferns from the United States. *Bulletin of the Torrey Botanical Club* 4: 11–12.

Faber-Langendoen, D. 2018. Northeast Regional Floristic Quality Assessment Tools for Wetland Assessments. NatureServe, Arlington, VA. 52 pp.

Fairbrothers, David E. and Mary Y. Hough. 1973. Rare or Endangered Vascular Plants of New Jersey. Science Notes No. 14, New Jersey State Museum, Trenton, NJ. 53 pp.

Farrar, Donald R. 1976. Spore retention and release from overwintering fern fronds. *American Fern Journal* 66(2): 49–52.

Fernald, M. L. 1950. *Gray's Manual of Botany*. Dioscorides Press, Portland, OR. 1632 pp.

Frances, Anne (Principal Investigator). 2017. Prioritization and Conservation Status of Rare Plants in the North Atlantic - Final Report. Report prepared for NatureServe by the North Atlantic Landscape Conservation Cooperative, Hadley, MA. Available at <https://www.natureserve.org/publications/prioritization-and-conservation-status-rare-plants-north-atlantic-final-report>

Gleason, H. A. and A. Cronquist. 1991. *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. Second Edition. The New York Botanical Garden, Bronx, NY. 910 pp.

Harvey, F. L. 1880. *Asplenium Bradleyi*. *Botanical Gazette* 5(2): 15.

Herraro, Alberto, Carmen Prada, Emilia Pangua, Adrian Escudero, Agustin Rubio, and Santiago Pajaron. 1993. Gametophyte morphology of four subspecies of *Asplenium trichomanes* L. *Botanica Complutensis* 18: 67–77.

Hill, Steven R. 2003. Conservation assessment for Bradley's Spleenwort (*Asplenium bradleyi* D. C. Eaton). Center for Biodiversity Technical Report 2003(1). Prepared for USDA Forest Service, Vienna, IL. 26 pp.

Homoya, Michael A., D. Brian Abrell, James R. Aldrich, and Thomas W. Post. 1985. The natural regions of Indiana. Indiana Natural Heritage Program, Department of Natural Resources, Indianapolis, IN. Available at <http://journals.iupui.edu/index.php/ias/article/view/8352>

Hough, Mary Y. 1983. *New Jersey Wild Plants*. Harmony Press, Harmony, NJ. 414 pp.

ITIS (Integrated Taxonomic Information System). Accessed August 2, 2022 at <http://www.itis.gov>

Kartesz, J. T. 2015. The Biota of North America Program (BONAP). Taxonomic Data Center. (<http://www.bonap.net/tdc>). Chapel Hill, NC. [Maps generated from Kartesz, J. T. 2015. Floristic Synthesis of North America, Version 1.0. Biota of North America Program (BONAP) (in press)].

Keesling, Jim. 2016. Photo of *Asplenium bradleyi* from Arkansas. Shared via iNaturalist at <https://www.inaturalist.org/observations/35111115>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

Kessler, Michael. 2010. Biogeography of Ferns. *In* K. Mehltreter, L. R. Walker, and J. M. Sharpe. Fern ecology. Cambridge University Press, Cambridge, United Kingdom. Available at https://www.zora.uzh.ch/id/eprint/42711/9/Kessler_Fern_Ecology_Book_2010.pdf

Lee, E. L. 1909. *Asplenium bradleyi* in north Alabama. The Fern Bulletin 17: 43–45.

Lee, E. L. 1911. Fern notes from the south. American Fern Journal 1: 49–51.

Leopold, Donald J. 2005. Native Plants of the Northeast: A Guide for Gardening and Conservation. Timber Press, Portland, OR. 308 pp.

Lyle, Laurina Isabella. 1980. A floristic and ecological survey of the pteridophytes of the northwestern highland rim, Kentucky and Tennessee. Master's Thesis, Austin Peay State University, Clarksville, TN. 61 pp.

Marchant, D. Blaine, Douglas E. Soltis, and Pamela S. Soltis. 2016. Patterns of abiotic niche shifts in allopolyploids relative to their progenitors. New Phytologist 212: 708–718.

Mid-Atlantic Herbaria. 2022. <https://midatlanticherbaria.org/portal/index.php>. Accessed on August 2, 2022.

Minicuci, Lee. 2019. *Asplenium montanum* Rare Plant Profile. New Jersey Department of Environmental Protection, Division of Parks and Forestry, New Jersey Forest Service, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 11 pp.

Mohlenbrock, Robert H. and Jane Hinnens Engh. 1964. Ferns and fern allies of Pine Hills field station and environs (Illinois). American Fern Journal 54: 25–38.

Montgomery, James D. 1982. Habitat preservation and rare pteridophytes in New Jersey. *In* William J. Cromartie (ed.). New Jersey's Endangered Plants and Animals. Stockton State College Center for Environmental Research, Pomona, NJ.

Montgomery, J. D. and D. E. Fairbrothers. 1992. New Jersey Ferns and Fern Allies. Rutgers University Press, New Brunswick, NJ. 293 pp.

Morlang, Charles Jr. 1967. Hybridization, polyploidy and adventitious growth in the genus *Asplenium*. *American Journal of Botany* 54(7): 887–897.

NatureServe. 2022. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed August 1, 2022 at <https://explorer.natureserve.org/>

Nayar, B. K. and S. Kaur. 1971. Gametophytes of homosporous ferns. *Botanical Review* 37(3): 295–396.

NJNHP (New Jersey Natural Heritage Program). 2010. Special Plants of NJ - Appendix I - Categories & Definitions. Site updated March 22, 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2022. Biotics 5 Database. NatureServe, Arlington, VA. Accessed February 1, 2022.

NYNHP (New York Natural Heritage Program). 2022a. Online conservation guide for *Asplenium montanum*. Available at <https://guides.nynhp.org/mountain-spleenwort/>.

NYNHP (New York Natural Heritage Program). 2022b. Online conservation guide for *Asplenium bradleyi*. Available <https://guides.nynhp.org/bradleys-spleenwort/>.

Ostlie, W. R. and A. Treher. 2018. *Asplenium bradleyi* conservation status factors. NatureServe, Arlington, VA. Accessed August 1, 2022 at https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.129065/Asplenium_bradleyi

Pangua, Emilia, Stuart Lindsay, and Adrian Dyer. 1994. Spore germination and gametophyte development in three species of *Asplenium*. *Annals of Botany* 73: 587–593.

PANHP (Pennsylvania Natural Heritage Program). 2019. Species and Natural Features List. Fact sheet for *Asplenium bradleyi* available at <https://www.naturalheritage.state.pa.us/factsheet.aspx?=15823>

Peck, James H. 2011. History of Arkansas pteridophyte studies with a new annotated checklist and floristic analysis. *Phytoneuron* 38: 1–39.

Pickett, F. L. 1914a. Some ecological adaptations of certain fern prothallia - *Camptosorus rhizophyllus* Link., *Asplenium platyneuron* Oakes. *American Journal of Botany* 1(9): 477–498.

Pickett, F. L. 1914b. The development of the prothallia of *Camptosorus rhizophyllus*. *Botanical Gazette* 57: 228–238.

POWO. 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Retrieved August 2, 2022 from <http://www.plantsoftheworldonline.org/>

Pretz, Harold W. 1911. An interesting find. *American Fern Journal* 1(6): 137–141.

- Raven, Peter H., Ray F. Evert and Susan E. Eichhorn. 1986. *Biology of Plants*. Worth Publishers, New York, NY. 775 pp.
- Rhoads, Ann Fowler and Timothy A. Block. 2007. *The Plants of Pennsylvania*. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.
- Schneller, Johann Jakob and Rolf Holderegger. 1996. Genetic variation in small, isolated fern populations. *Journal of Vegetation Science* 7: 113–120.
- Smith, Dale M., Truman R. Bryant, and Donald E. Tate. 1961. Another *Asplenium* Hybrid from Kentucky. *American Fern Journal* 51(2): 70–73.
- Snyder, David B. 1984. Botanical Discoveries of Vincent Abraitys. *Bartonia* 50: 54–56.
- Testo, Weston L. and James E. Watkins Jr. 2011. Comparative development and gametophyte morphology of the Hart’s-tongue Fern, *Asplenium scolopendrium* L. *Journal of the Torrey Botanical Society* 138(4): 400–408.
- Tompkins, Robert. 2018. Vascular flora of Crowders Mountain State Park. *Castanea* 83(2): 236–248.
- Tuttle, Mary Louise. 1915. Fern trips in Virginia. *American Fern Journal* 5: 108–113.
- U. S. Army Corps of Engineers. 2020. National Wetland Plant List, version 3.5. https://cwbi-app.sec.usace.army.mil/nwpl_static/v34/home/home.html U. S. Army Corps of Engineers Research and Development Center, Cold Regions Research and Engineering Laboratory, Hanover, NH.
- USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2022a. *Asplenium bradleyi* illustration from Britton, N. L. and A. Brown, 1913, *An illustrated flora of the northern United States, Canada and the British Possessions*, 3 vols., Kentucky Native Plant Society, New York, Scanned By Omnitek Inc. Image courtesy of The PLANTS Database (<http://plants.usda.gov>). National Plant Data Team, Greensboro, NC.
- USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2022b. PLANTS profile for *Asplenium bradleyi* (Bradley's Spleenwort). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed August 2, 2022 at <http://plants.usda.gov>
- Wagner, Warren H. Jr. 1954. Reticulate evolution in the Appalachian *Aspleniums*. *Evolution* 8: 103–118.
- Wagner, W. H. Jr. 1983. Edgar T. Wherry and his contributions to pteridology. *American Fern Journal* 73(1): 1–5.

Wagner, W. H. Jr., F. S. Wagner, Joseph A. Lankalis, and James F. Matthews. 1973. *Asplenium montanum* x *platyneuron*, a new primary member of the Appalachian spleenwort complex from Crowder's Mountain, N. C. *Journal of the Elisha Mitchell Scientific Society* 89(3): 218–223.

Wagner, Warren H. Jr., Robbin C. Moran, and Charles R. Werth. Page updated November 5, 2020. *Asplenium bradleyi* D. C. Eaton. In: *Flora of North America* Editorial Committee, eds. 1993+. *Flora of North America North of Mexico* [Online]. 22+ vols. New York and Oxford. Accessed July 28, 2022 at http://floranorthamerica.org/Asplenium_bradleyi

Walz, Kathleen S., Linda Kelly, Karl Anderson and Jason L. Hafstad. 2018. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservatism (CoC) Values for Species and Genera. New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ. Submitted to United States Environmental Protection Agency, Region 2, for State Wetlands Protection Development Grant, Section 104(B)(3); CFDA No. 66.461, CD97225809.

Wang, B., and Y. L. Qiu. 2006. Phylogenetic distribution and evolution of mycorrhizas in land plants. *Mycorrhiza* 16(5): 299–363.

Waters, C. E. 1920. The society for the prevention of the wild. *American Fern Journal* 10(4): 115–119.

Weakley, A. S. 2015. *Flora of the southern and mid-Atlantic states*, working draft of May 2015. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC.

Weber, Wallace R. and Robert H. Mohlenbrock. 1958. An unusual form of *Asplenium bradleyi*. *American Fern Journal* 48(4): 159–161.

Werth, Charles R., Sheldon I. Guttman, and W. Hardy Eshbaugh. 1985. Electrophoretic evidence of reticulate evolution in the Appalachian *Asplenium* complex. *Systematic Botany* 10(2): 184–192.

Wherry, Edgar T. 1920. Soil reactions of certain rock ferns: II. *American Fern Journal* 10(2): 45–52.

Wherry, Edgar T. 1925. The Appalachian *Aspleniums*. *American Fern Journal* 15(2): 46–54.

Wherry, Edgar T. 1928. Ferns at Dripping Spring, Oklahoma. *American Fern Journal* 18: 61–63.

Wherry, Edgar T. 1931. *Asplenium bradleyi* erroneously reported growing on limestone again. *American Fern Journal* 21: 111-113.

Wherry, Edgar T. 1935. Fern field notes, 1935. *American Fern Journal* 25(4): 123-126.

Wherry, Edgar T. 1957. Which northeastern ferns are evergreen? *American Fern Journal* 47(3): 93–95.

Williamson, John. 1878. *Ferns of Kentucky*. J. P. Morton and Co., Louisville, KY. 154 pp.

Wubs, E. R. Jasper, G. Arjen de Groot, Heinjo J. During, Johannes C. Vogel, Michael Grundmann, Piet Bremer, and Harald Schneider. 2010. Mixed mating system in the fern *Asplenium scolopendrium*: implications for colonization potential. *Annals of Botany* 106: 583–590.