Listera smallii

Appalachian Twayblade

Orchidaceae

Listera smallii courtesy Alan Cressler, Lady Bird Johnson Wildflower Center

Listera smallii 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

Listera smallii (Appalachian Twayblade) is a fibrous-rooted perennial orchid. *Listera* is a relatively small genus that contains only 25 species worldwide, eight of which occur in North America (Magrath and Coleman 2020). Twayblades have a single pair of stalkless leaves near the middle of the stem. The plants are generally small and inconspicuous so close examination is needed to appreciate their charms (Slaughter 2007), although Chubb (1941) remarked that *L. smallii* was one of the most attractive plants she had observed during a botanical field trip. The flowers of Appalachian Twayblade come in an assortment of "subdued earth colors" (Fowler 2005) including green, whitish, yellowish, pinkish-tan, purple-brown, caramel, or cinnamon (Small 1897, Barksdale 1933, Correll 1937, Godfrey and Wooten 1981, Brown 2008, Magrath and Coleman 2020).

The slender stems of *Listera smallii* may range from 5–35 cm in height and its dark green leaves are slightly kidney-shaped. The stems are mostly smooth but some glandular hairs are usually present near the top. The inflorescence is a loose raceme of 5–15 flowers on stalks about 6–7 mm long. The three narrow sepals are strongly reflexed and the two upper petals are linear. The prominent lower petal (lip) is 6–10 mm long and 5–7 mm wide with two small teeth near the base and its outer third is split into two spreading, rounded lobes. Mature capsules are about 5 mm long and semi-erect. (See Wiegand 1899, Britton and Brown 1913, Fernald 1950, Godfrey and Wooten 1981, Gleason and Cronquist 1991, Magrath and Coleman 2020). Two other species of *Listera* occur in New Jersey, *L. australis* and *L. cordata*, but the lips of those species are more deeply divided and end in pointed lobes (Rhoads and Block 2007, Weakley et al. 2022).

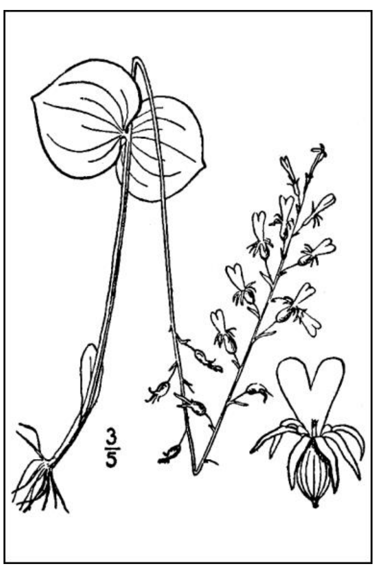


Illustration from Britton and Brown 1913, courtesy USDA NRCS 2023a. Photos by Stephanie Brundage (center) and Alan Cressler (right), courtesy Lady Bird Johnson Wildflower Center.

Like many orchids, *Listera smallii* must rely heavily on vegetative propagation to maintain populations. Appalachian Twayblade is thought to be a long-lived species (Morse 1983). *Listera* plants have rhizomes that generate new stems during the growing season, and the genus is unusual in that some stems can also be produced by buds that develop on the roots (Dressler

1981, Rasmussen 1995). Either fertile or sterile shoots may develop so a colony is likely to contain a mixture of both flowering and nonflowering plants (Henry and Buker 1955, Buker 1979). Throughout its range, *Listera smallii* flowers during June or July (Correll 1937, Massey 1953, Fowler 2005, Rhoads and Block 2007). Hough (1983) noted that fruits are present in August. Aboveground portions of the plant die back at the end of the season (Gibson 1961).

Listera smallii is uncommon and has a restricted range so research on the biology of the species has been limited. However, molecular data suggests that *L. smallii* is closely related to *L. cordata* and *L. ovata* (Zhou and Jin 2018), two widely distributed species. Consequently, information gleaned from investigations of its more abundant relatives may provide some insight regarding the reproduction and development of Appalachian Twayblade.

Pollinator Dynamics

Listera flowers are pollinated by insects that are drawn to shallow nectaries situated near the base of the lip. Darwin (1890) noted that his son was struck by the number of webs constructed above the plants, as if spiders were aware of how attractive *Listera* was to insects. The specific pollinators of *L. smallii* are unknown (Fowler 2005, Pace 2020) but the odors produced by twayblades—generally unpleasant to humans—suggest fly pollination, and some *Listera* species are also visited by nectar-seeking wasps (Dressler 1981). *L. cordata* is primarily pollinated by fungus gnats (Ackerman and Mesler 1979), while ichneumon wasps and solitary bees have been reported as pollinators of *L. ovata* (Burns-Balogh et al. 1987). Brys et al. (2008) investigated the impact of population size on reproductive success in *L. ovata*, finding that 30–40 flowering plants was optimal for pollination efficiency and fruit set.

Listera flowers utilize an explosive mechanism to facilitate cross-pollination by insects. While feeding on the nectar, the insects come into contact with minute trigger hairs on the rostellum (a flap of tissue that initially enfolds the pollinia and conceals the stigma). Contact with a hair triggers the rapid ejection of a tiny drop of sticky liquid onto the insect followed by the immediate release of the pollinia which adhere to the quick-drying droplet. The rostellum simultaneously unfurls and covers the stigma, and after the insect exits it carries the pollinia to another flower. After about a day the rostellum lifts and exposes the receptive stigma to new visitors. When pollinia come into contact with stigmas they break into chunks, so a single insect may fertilize several flowers with the same pollen mass. (See Baldwin 1884, Darwin 1890, Ackerman and Mesler 1979, Burns-Balogh et al. 1987).

Both *L. cordata* and *L. ovata* are self-compatible (Ackerman and Mesler 1979, Brys et al. 2008). Although the movements of the rostellum reduce the likelihood of self-pollination, some *Listera* flowers may be fertilized with pollen from another flower on the same plant. A study of *L. cordata* also found that when pollinia have not been removed after four days the rostellum lifts anyway, exposing the stigma and increasing the chances of receiving closely related pollen (Ackerman and Mesler 1979).

Seed Dispersal and Establishment

Studies of fertility in related species suggest that a single *Listera smallii* plant can probably produce thousands of seeds. Stoutamire (1964) counted 376 seeds in a *Listera cordata* capsule and calculated that a typical inflorescence would produce 2,860 seeds based on an average of 7.6 capsules per plant. Nazarov and Gerlach (1997) projected a high reproductive potential for *L. ovata* based on the number of ovules per flower, which ranged from 532–2165 (mean 1410).

Orchid seeds lack endosperm and consist mainly of an embryo surrounded by a loose, papery coating (Dressler 1981). The tiny propagules are often referred to as dust seeds, although their structure suggests that they function like small, light balloons. The design facilitates wind dispersal because the relatively large spaces within the seeds allow them to float in the air for long periods. The seeds of many *Listera* species can also remain afloat in water for several seconds (Arditti and Ghani 2000). Arditti and Ghani observed that the general characteristics of orchid seeds might additionally permit their transport by adherence to birds or mammals.

Dormancy in orchid seeds varies between species, ranging from 0–7 years (Eriksson and Kainulainen 2011). Dressler (1981) noted that the seeds of orchids may survive for long periods if they are cool and dry. When the seeds become hydrated, limited metabolic activity is initiated but germination requires appropriate physical conditions and, in nature, the right kind of fungi Prior to leaf development, orchid seedlings are completely dependent on their fungal partners for nutrients (Dressler 1981). Some types of orchids rely on mycorrhizae only during the establishment phase while others continue to need fungal associations throughout their lives (Eriksson and Kainulainen 2011). *Listera ovata* can form associations with multiple types of fungi and no correlation has been found between fungal community composition and germination (Jacquemyn et al. 2015). Mature *L. cordata* plants often associate with fungi in the genus *Rhizoctonia* (Nieuwdorp 1972, Rasmussen 1995) and form typical orchid-type mycorrhizae (Harley and Harley 1987). Rasmussen (1995) suggested that the presence of mycorrhizae could allow fragments of an orchid's roots to persist in the soil for some time.

Many orchids develop slowly and that is likely to be the case for *Listera smallii*. In both *L. ovata* and *L. cordata* the roots are produced first and the plants remain below the surface for 3–4 years before generating their first green leaves (Jacquemyn et al. 2015, Kotilínek et al. 2018). *L. ovata* plants can remain in the juvenile stage for up to five years before they begin to flower (Brzosko 2002).

Habitat

Listera smallii is found at high elevations in the Appalachian Mountains, typically around 600–1300 meters above sea level (Magrath and Coleman 2020). Characteristic habitats include moist woods, damp thickets, swamps, or bogs (Jennison 1935, Correll 1937, Massey 1953, Godfrey and Wooten 1981, Hough 1983, Rhoads and Block 2007, Rossell et al. 2016). *L. smallii* has been reported in an assortment of climax forest types including communities that were dominated by hardwoods, evergreens, or mixed species (Davis 1930, Morse 1983, Weakley and Schafale 1994, Western Pennsylvania Conservancy 2006). Appalachian Twayblade is tolerant of deeply shaded locations where few other herbaceous species can grow so the ground cover at sites where it occurs is often notably sparse (Harshberger 1903, Braun 1935, Duncan 1948, Weakley and Schafale 1994, Western Pennsylvania Conservancy 2006). In some sites *Listera smallii* has been known to co-occur with *L. cordata* (Kokesh 1988, NJNHP 2022).

There are a number of records of *Listera smallii* from Appalachian balds. Those communities are drier than the orchid's typical habitat and lack a tree canopy, instead supporting a dense cover of shrubs or herbaceous vegetation (Schafale and Evans 2014). *L. smallii* has been found on *Rhododendron*-dominated heath balds, on balds where other shrubby species prevail, and on grass balds (Ramseur 1960, Schafale and Weakley 1990), including one that had been cleared for the construction of a fire tower (Mark 1959). *Listera smallii* has also long been known to occur in West Virginia's Cranberry Glades region, a high-elevation complex of bog forest, shrub thickets, and open glades (Netting 1932, Darlington 1943, Clarkson 1966, Kokesh 1988).

In New Jersey, *Listera smallii* is situated in a *Rhododendron* thicket near the edge of a swamp (NJNHP 2022). Throughout its range, *L. smallii* has often been noted as growing beneath *Rhododendron* (eg. Harshberger 1903, Braun 1935, Correll 1937, Duncan 1948, DuMond 1970, Buker 1979, Weakley and Schafale 1994, Muzika et al. 1996, Vandermast and Van Lear 1999, Fowler 2005, Western Pennsylvania Conservancy 2006). Numerous notations on herbarium sheets have also indicated an association between the orchid and rhododendrons (Mid-Atlantic Herbaria 2023). *Rhododendron maximum* was frequently specified but in some instances the orchid was found under *R. catawbiense*. Vandermast and Van Lear (2002) noted that *L. smallii* was "apparently obligated" to grow beneath *Rhododendron*, and current floras indicate that it "often" or "nearly always" does so (Magrath and Coleman 2020, Weakley et al. 2022).

Listera smallii belongs to a tribe in the orchid family (Neottieae) in which mycoheterotrophy is relatively common (Zhou and Jin 2018). Mycoheterotrophic plants typically lack chlorophyll and are reliant on fungal associations for carbon. Some plants with green leaves can be partial mycoheterotrophs, fixing some carbon on their own but supplementing it with carbon that is obtained from other nearby species and transferred via the local fungal network. Schiebold et al. (2017) recently documented partial mycoheterotrophy in the closely related *Listera cordata* and it may be that *Listera smallii* can also utilize carbon from external sources, thereby allowing it to flourish in sites like *Rhododendron* thickets where light availability is limited.

Wetland Indicator Status

Listera smallii is a facultative wetland species, meaning that it usually occurs in wetlands but may occur in nonwetlands (U. S. Army Corps of Engineers 2020).

USDA Plants Code (USDA, NRCS 2023b)

LISM

Coefficient of Conservancy (Walz et al. 2020)

CoC = 10. Criteria for a value of 9 to 10: Native with a narrow range of ecological tolerances, high fidelity to particular habitat conditions, and sensitive to anthropogenic disturbance (Faber-Langendoen 2018).

Distribution and Range

The global range of *Listera smallii* is restricted to the east-central United States, where it mainly occurs in the Appalachian Mountains (Core 1932, Bartgis et al. 2015, POWO 2023). The map in Figure 1 depicts the extent of Appalachian Twayblade in North America.

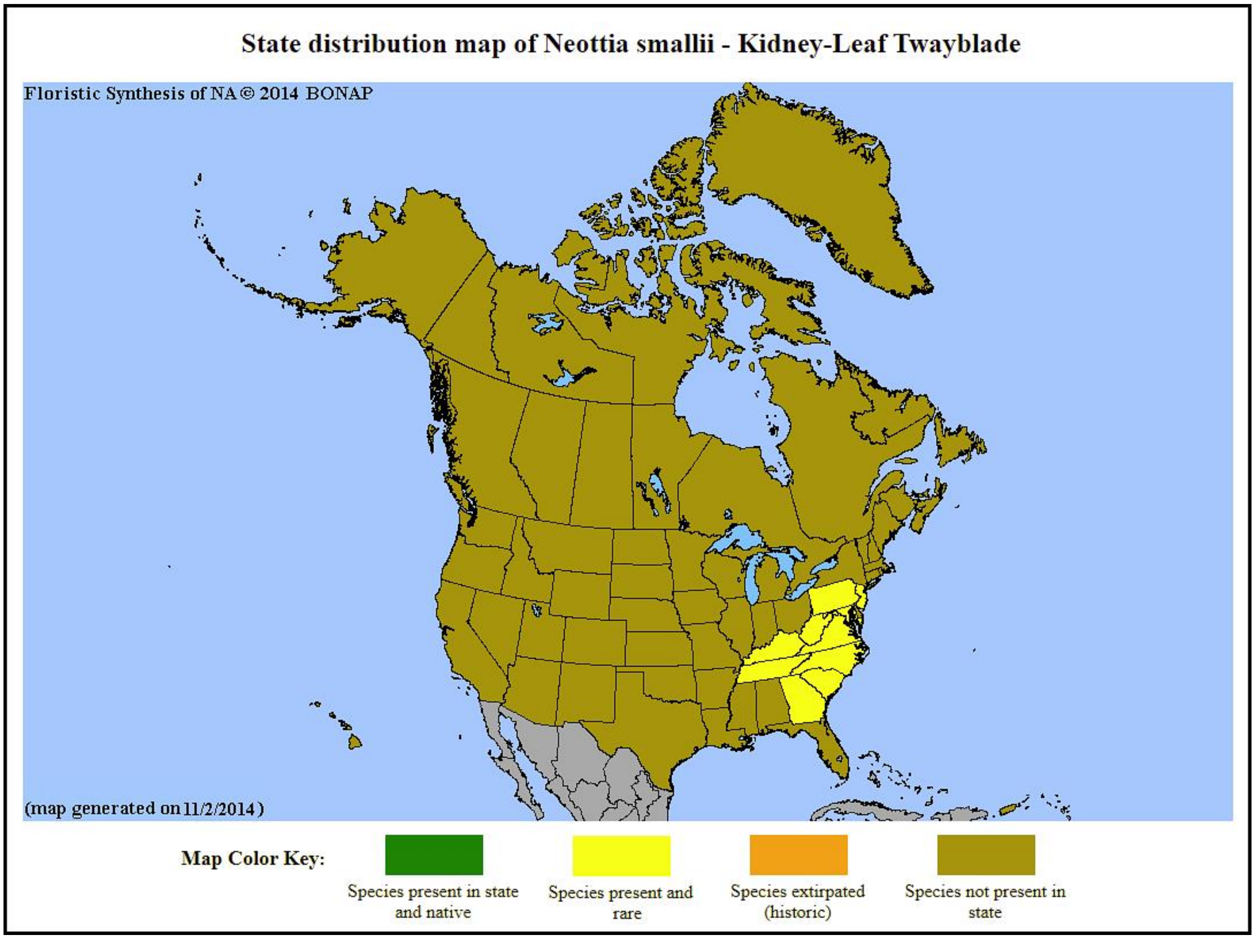

Figure 1. Distribution of L. smallii in North America, adapted from BONAP (Kartesz 2015).

The USDA PLANTS Database (2023b) shows records of *Listera smallii* in two New Jersey counties: Hudson and Sussex (Figure 2 below). The only confirmed records of Appalachian Twayblade in the state are from Sussex County and no documentation was found of a Hudson County occurrence (NJNHP 2022).

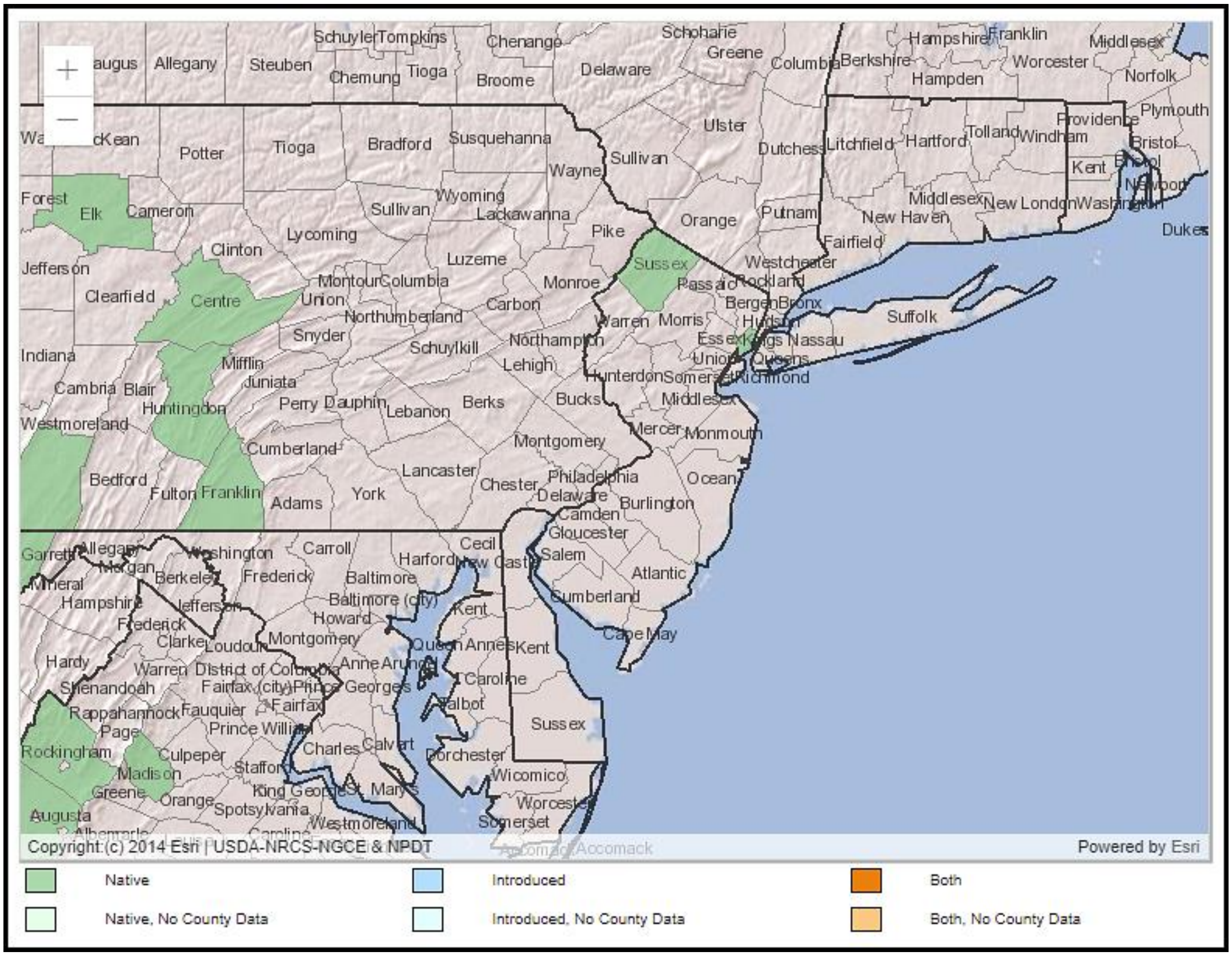

Figure 2. County records of L. smallii in New Jersey and vicinity (USDA NRCS 2023b).

Conservation Status

Listera smallii 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 2023). The map below (Figure 3) illustrates the conservation status of *L. smallii* throughout its range. Appalachian Twayblade is not considered secure in any of the states where it occurs. The species is critically imperiled (very high risk of extinction) in four states, imperiled (high risk of extinction) in three states, and vulnerable (moderate risk of extinction) in three states.

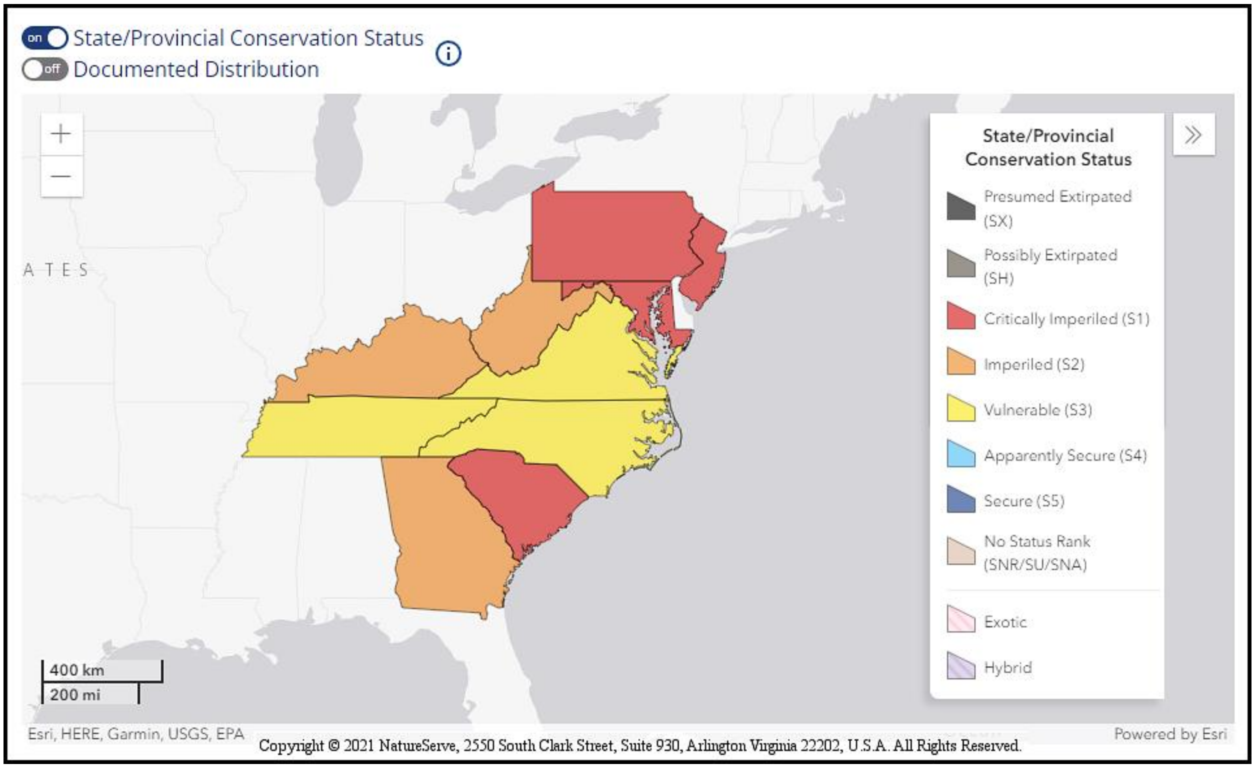

Figure 3. Conservation status of L. smallii in North America (NatureServe 2023).

Listera smallii is ranked S1.1 in New Jersey (NJNHP 2022), meaning that it is critically imperiled due to extreme rarity. A species with an S1.1 rank has only ever been documented at a single location in the state. *L. smallii* 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 such as wetlands or coastal habitats, being listed does not currently provide broad statewide protection for the plants. Additional regional status codes assigned to *L. smallii* signify that the orchid is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Although *Listera smallii* was known from more southern localities at the end of the 1800s (Small 1897) the orchid was not discovered in New Jersey until the 1950s (NJNHP 2022). *L. smallii* was one of the earliest plants to be labeled as endangered in the state because the sole occurrence was isolated and situated at the northern edge of the species' range (Fairbrothers and Hough 1973). The population was relatively vigorous throughout the 20th century and has persisted at the same location for decades, but it was recently noted that the site of the occurrence may be vulnerable to beaver activity (NJNHP 2022).

Threats

Listera smallii is imperiled or vulnerable throughout its entire range, and Morse (1983) observed that few occurrences of the species were appropriately managed or protected. As with many other forest or wetland plants, the habitat of *L. smallii* can be altered by human activities such as canopy removal, wetland drainage, or stream impoundment, making it unsuitable for the orchids (Morse, 1983, KRPD 2018, Chafin 2020, Frye 2021). *Listera smallii* is also subject to illegal collection—Summerfield (2020) noted that Appalachian Twayblade is frequently targeted by plant poachers.

Humans are not the only mammals that threaten *Listera smallii* populations. The species is known to be damaged by deer (Miller et al. 1992), and habitat destruction resulting from the activity of feral hogs has been identified as a problem in parts of the orchid's range (Rossell et al. 2016, Chafin 2020). Abraitys (1980) reported that many rare plant communities in northern New Jersey had been flooded by beavers, although at the time of his report the *L. smallii* population appeared to be secure. More recent observations from the site indicated that beavers have become active in the vicinity of the *L. smallii* population and flooding was noted within about 300 meters of the occurrence (NJNHP 2022).

Because *Listera smallii* often has a close association with *Rhododendron maximum*, populations of the orchid could be threatened by *Rhododendron* loss. The shrub appears to be facing a number of threats in the Appalachian region. Baird et al. (2013) indicated that in recent decades *R. maximum* colonies had been dying for unknown reasons and various nematodes were under investigation as a possible cause. Deliberate removal of some *Rhododendron* populations in the southern Appalachians was also under consideration as a means to promote the growth of hardwood trees (Dudley 2018).

Some of the challenges facing *Listera smallii* may be exacerbated by climate change, although there is presently insufficient information available to evaluate the species' level of vulnerability. Critical details regarding the twayblade's pollinators, mycorrhizal relationships, and drought tolerance are lacking. Although the specifics of the relationship between *L. smallii* and *Rhododendron maximum* are not well-understood, the orchid's susceptibility to changing climactic conditions may be partially tied to the fate of the shrub. Dudley et al. (2020) identified *R. maximum* as a foundational species that has the potential to increase the resistance and resilience of the ecosystems it inhabits, so adaptability of the rhododendron could secondarily benefit *Listera smallii*. Unfortunately, it seems that *R. maximum* is sensitive to droughts (Lipp and Nilsen 1997), which are increasing in both frequency in duration in New Jersey as global temperatures continue to rise (Hill et al. 2020).

Management Summary and Recommendations

Although *Listera smallii* is listed as apparently secure (G4) at a global scale, the rank was based on data from 1983 and the twayblade's status is in need of review (NatureServe 2023). Current state rankings indicate a significant level of vulnerability throughout its range (Figure 3), making the species a priority for conservation. Although *L. smallii* has sometimes been found in drier, more open habitats the orchid seems to have a particular affinity for moist *Rhododendron* thickets. Consequently, effective management of Appalachian Twayblade may require the preservation of entire communities in order to maintain extant orchid populations and provide suitable habitat for the establishment of new colonies. Canopy disturbance should be avoided and every effort should be made to maintain natural site hydrology.

Listera smallii populations can fluctuate in size from one year to the next (NJNHP 2022) so monitoring of occurrences should focus on habitat quality rather than the quantity of plants. Site evaluations might also consider the extent of comparable habitat in the vicinity that could be utilized by *L. smallii* in the future. It is difficult to detect herbivory in small, inconspicuous plants like twayblades but any signs of disturbance should be noted.

The lack of species-specific information regarding *Listera smallii* is an impediment to effective management planning. The orchid's pollinators have not been identified (NAOCC 2023) and the establishment requirements of the species do not appear to have been studied in either natural or controlled settings. Research on mycorrhizal associations should be prioritized because it might shed some light on the apparent relationship between *L. smallii* and *Rhododendron*, which in turn could enhance understanding of some factors that govern colonization of new sites and help to predict the orchid's prospects for adapting to climate change.

Synonyms

The accepted botanical name of the species is *Listera smallii* Wiegand. Orthographic variants, synonyms, and common names are listed below (ITIS 2023, POWO 2023, USDA NRCS 2023b). A number of current sources utilize the synonym *Neottia smallii* (eg. Kartesz 2015, Brown 2020, ITIS 2023, POWO 2023, Weakley et al. 2022).

Botanical Synonyms	**Common Names**
Bifolium smallii (Wiegand) Nieuwl.	Appalachian Twayblade
Listera smallii f. *variegata* P. M. Br.	Kidneyleaf Twayblade
Neottia smallii (Wiegand) Szlach.	Small's Twayblade
Ophrys smallii (Wiegand) House	

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Listera smallii (right) with *Goodyera pubescens* by Alice Lounsberry, public domain image.