

# *Silene nivea*

Snowy Catchfly

Caryophyllaceae



*Silene nivea* by Nate Martineau, 2021

## ***Silene nivea* 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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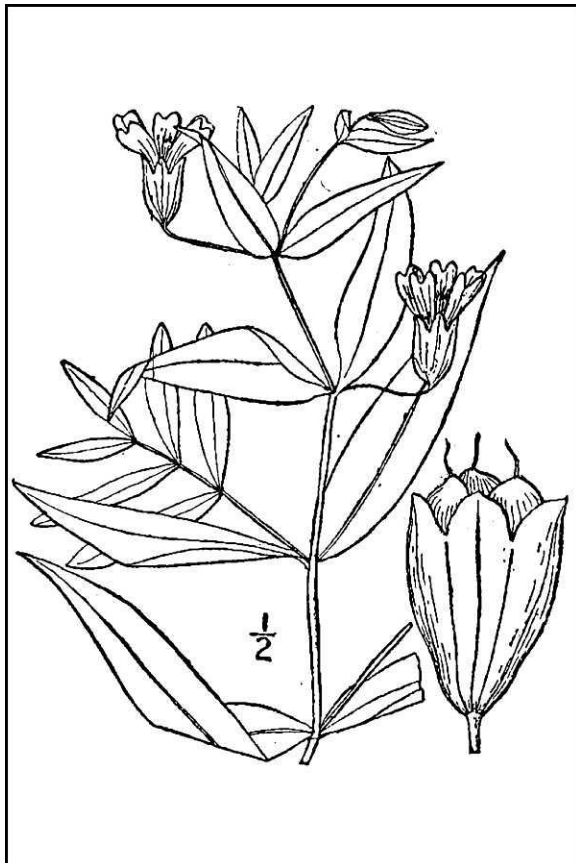
May, 2023

For:  
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This report should be cited as follows: Dodds, Jill S. 2023. *Silene nivea* 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, Trenton, NJ. 19 pp.

## Life History

*Silene nivea* (Snowy Catchfly) is a rhizomatous perennial herb in the Caryophyllaceae. The plants reproduce vegetatively from long rhizomes so some fairly large populations may consist of a single clone (MNDNR 2023). The 20–70 cm tall stems are erect or lean slightly outward and they are mostly smooth or slightly hairy at the upper end. The thin, green, lance-shaped leaves are arranged in pairs along the stem: They have smooth edges, pointed tips, and rounded bases with very short petioles or none at all. The long-stalked flowers grow singly in the leaf axils. The calyx on an *S. nivea* flower consists of five sepals which are fused for most of their length, forming an inflated green tube 14–17 mm long that has 10 inconspicuous veins and is strongly constricted at the base. The 3-styled ovary is elevated on a short (5–6 mm) stalk, to which the 10 stamens and 5 white petals are also attached. Each petal has a narrow basal claw as long as the calyx tube and an expanded upper portion that extends for another 6–7 mm and is notched at the tip. A small, indented appendage 1–1.6 mm long is present at the base of the petal's expanded limb. (See Nuttall 1818, Britton and Brown 1913, Fernald 1950, Gleason and Cronquist 1991, Morton 2020). *Silene nivea* usually blooms during June or July (Weakley et al. 2022). The fruits appear to develop promptly, as both flowering and fruiting plants have been observed simultaneously in New Jersey populations (NJNHP 2022).



Left: Britton and Brown 1913, courtesy USDA NRCS 2023a.

Right: Nate Martineau, 2021.

*Silene nivea* is most likely to be confused with Bladder Campion (*Silene vulgaris*), an introduced and weedy species. Bladder Campion differs in several ways: The leaves of the inflorescences

are reduced and bractlike, the calyx tubes are not contracted at the base, the petal appendages are absent or diminutive (< 0.2 mm long), and the stalks of the ovaries are only 2–3 mm in length (Morton 2020, Weakley et al. 2022).



Left: Flower by Nate Martineau, 2021.



Right: Developing fruit by Peter M. Dziuk, 2013.

Nuttall (1818) inferred a close relationship between *S. nivea* and *S. vulgaris* due to their morphological similarity. Based on a molecular study of selected North American *Silene* species, Burleigh and Holtsford (2003) reported that *Silene nivea* was likely related to *S. stellata* and *S. regia*. However, Popp and Oxelman (2007) reached different conclusions following a broader investigation, suggesting instead that *S. nivea* had no close relatives among the North American *Silene* species but was closely aligned with a European species (*S. baccifera*) that has a berry-like fruit and a climbing habit. Unfortunately, *S. vulgaris* was not included in either study so Nuttall's opinion cannot be confirmed or refuted. *Silene nivea* is tetraploid (Kruckeberg 1964), raising the possibility that the species originated as a hybrid. Some species of *Silene* are known to hybridize in nature (Mitchell and Uttal 1969), although experimental crosses between *S. nivea* and other species did not yield fertile offspring (Kruckeberg 1964).

### **Pollinator Dynamics**

Little specific information is available regarding the pollinators of *Silene nivea*, although extensive research has been conducted on pollination in the genus. For example, Jürgens et al. (2002a) studied sexual reproduction in 64 other *Silene* species. *Silene* is a huge genus that includes about 700 species worldwide, and the diversity of floral characteristics within the genus is indicative of multiple pollination syndromes (Stebbins 1970, Morton 2020). Some *Silene* spp. attract mainly nocturnal pollinators while others are pollinated primarily by diurnally active insects or birds; a few species are almost entirely self-pollinated but many appear to be capable of facultative self-fertilization (Jürgens et al. 1996, Jürgens 2006).

The majority of *Silene* species probably utilize multiple pollinators but floral structure, coloration, and size are clues as to which ones are most important or effective (Jürgens 2006, Reynolds et al. 2009). The light coloration and long floral tubes of *Silene nivea* suggests that long-tongued nocturnal insects such as large moths are likely to be its principal pollinators, although no information was found regarding what time the flowers open or whether they produce a scent. Most night-flowering *Silene* plants produce floral scent compounds comparable to those of moth-pollinated blooms in other families (Jürgens et al. 2002b). Research on other *Silene* species has shown that flowers which remain open around the clock can be successfully pollinated by both diurnal and nocturnal insects regardless of their primary syndrome, and at least one (*Silene otites*) is known to change its scent during the course of the day to attract a different suite of visitors (Jürgens et al. 1996, Dötterl et al. 2012). Daytime pollinators of *Silene nivea* are likely to include bees. Robertson (1929) observed a single halictid bee (*Lasioglossum pilosus pilosus*) on *S. nivea*, and bumblebees (*Bombus* spp.) have been found on *Silene* plants with similar flower structure such as *S. latifolia* and *S. vulgaris* (Stubbs et al. 1992). Flies and wasps have also been reported as diurnal pollinators of those species (Jürgens et al. 1996, Young 2002). Young (2002) manipulated pollinator access to *S. latifolia* and demonstrated that flowers exposed only to nocturnal visitors developed significantly more seeds than those restricted to diurnal pollinators. Despite the higher efficiency of moths as pollinators of its floral type, a study of *S. vulgaris* found that multiple visits are still required in order for the flowers to achieve full seed set (Pettersson 1991).

There is a particular relationship between moths in the genus *Hadena* and certain *Silene* flowers that can be simultaneously beneficial and harmful to the plants. In a process known as nursery pollination, female moths gather nectar and pollinate the plants but then they lay eggs inside the flowers and their larvae eat the developing seeds. Male moths of the same species provide pollination services without the cost (Kephart et al. 2006, Labouche and Bernasconi 2010). Nursery pollination by several species of *Hadena* has been reported for *Silene vulgaris* and *S. latifolia* in Europe where the plants are native (Jürgens et al. 1996, Dötterl et al. 2006). In the eastern United States, a comparable relationship exists. *Hadena ectypa* (Campion Coronet) is a nursery pollinator of *Silene stellata* and *S. vulgaris* (Nelson 2012, Milus 2017, Zhou et al. 2020). Both plant species have a suite of characteristics that favor moth pollination as well as a large, inflated calyx that provides sufficient space and shelter for developing larvae (Nelson 2012). Similar traits occur in *Silene nivea*, suggesting that its flowers might also be visited by *Hadena* moths. *Hadena ectypa* was documented in both Virginia and Massachusetts fairly recently (eg. Nelson 2012, Zhou et al. 2020) and the species was previously found in New Jersey although its presence in the state has not been confirmed since the 1970s (Schweitzer et al. 2018). *Hadena capsularis* (Capsule Moth) is also known to feed on flowers and seedheads of *Silene* spp., and a range map suggests that it too could occur in New Jersey (BugGuide 2023, NAMPG 2023).

### **Seed Dispersal**

*Silene nivea* fruits are capsules that equal the length of the calyx and open from the top at maturity, forming three broad teeth that sometimes split to make six. *Silene* species typically produce 15–100 seeds per flower. The seeds of *S. nivea* are brown to black with a rough surface and a diameter of less than 1 mm (Morton 2020).

The capsules of *Silene nivea* often remain on the stems through the winter months (Levine 1995). In similar species the seeds are primarily gravity-dispersed, often after being dislodged from the capsules by wind or passing animals (Montesinos et al. 2006, Barluenga et al. 2011). Jongejans and Schippers (1999) found that the seeds of *S. latifolia* seldom traveled more than a meter from the source plants. The seeds of plants along waterways may sometimes be transported for longer distances by flotation—McAtee (1918) noted that *S. nivea* populations on islands in the Potomac River were probably established by propagules that had been carried downstream.

No information was found about seed longevity, germination, or establishment in *Silene nivea*. Seed banking has been documented in a number of other species (Gross 1990). Plants in the genus *Silene* vary widely in their germination requirements: Some require a period of cold stratification while others do not, and certain species are strongly influenced by light or temperature (Baskin and Baskin 1988, Deno 1993 and 1996, Keller and Kollmann 1999). The diversity within the genus makes it difficult to draw conclusions about *S. nivea*.

When experimentally inoculated with a potential fungal partner *Silene nivea* was relatively unresponsive and no increase in biomass resulted (Boerner 1992), and the author noted that the plants in the Caryophyllaceae are generally only weakly mycotrophic. Only about half of the *Silene* species reviewed by Wang and Qiu (2006) were mycorrhizal.

## **Habitat**

*Silene nivea* is usually found in moist, wet, or flood-prone habitats at elevations of 0–400 meters above sea level (Morton 2020). The species is frequently located in sandy or rocky floodplains of rivers or creeks which may sometimes be scoured or receive fresh deposits of alluvial soils (Wheeler 1902, Crandall and Dolan 1997, Madsen 2006, Rhoads and Block 2007, Scott 2009, Angelo and Boufford 2011, Weakley et al. 2022). All of New Jersey's occurrences are situated along the banks of the Delaware River (NJNHP 2022). In Wisconsin, some streamside sites are very close to the water table and may become swampy (Hartley 1960). Other populations of *S. nivea* have been associated with seepage areas or springs (MNDNR 2003, Thompson 2010, Lynch and Weckwerth 2017), and occurrences have been reported from fen communities in Iowa, Minnesota, and Illinois (Nekola 1994, MNDNR 2003, Murphy et al. 2021). One Michigan habitat was described as an open riverside beach (Trull and Shackleford 2018).

Canopy cover is variable, ranging from open (Lammers 1983) to shaded (Angelo and Boufford 2011). In Iowa, Lynch and Weckwerth (2017) found *Silene nivea* in three forested seeps of varying ages. In addition to woodlands, *S. nivea* can occur in shrub thickets or meadows (Wheeler 1902, Braun 1934, Kost et al. 2007, Rhoads and Block 2007, Ruch et al. 2008 and 2013, Murphy et al. 2021). One Kentucky population was growing in a late successional old field (Abbott et al. 2001), and the habitat of an Indiana occurrence was described as a roadside, old field, and drier woodland edge (Ruch et al. 2015). According to Gottlieb et al. (1994), *S. nivea* has some tolerance for disturbed habitats.

## Wetland Indicator Status

The U. S. Army Corps of Engineers divided the country into a number of regions for use with the National Wetlands Plant List and portions of New Jersey fall into three different regions (Figure 1). *Silene nivea* has more than one wetland indicator status within the state. In the Northcentral and Northeast region, *S. nivea* is a facultative wetland species, meaning that it usually occurs in wetlands but may occur in nonwetlands. In other regions of the state it is facultative, meaning that it occurs in both wetlands and nonwetlands (U. S. Army Corps of Engineers 2020).

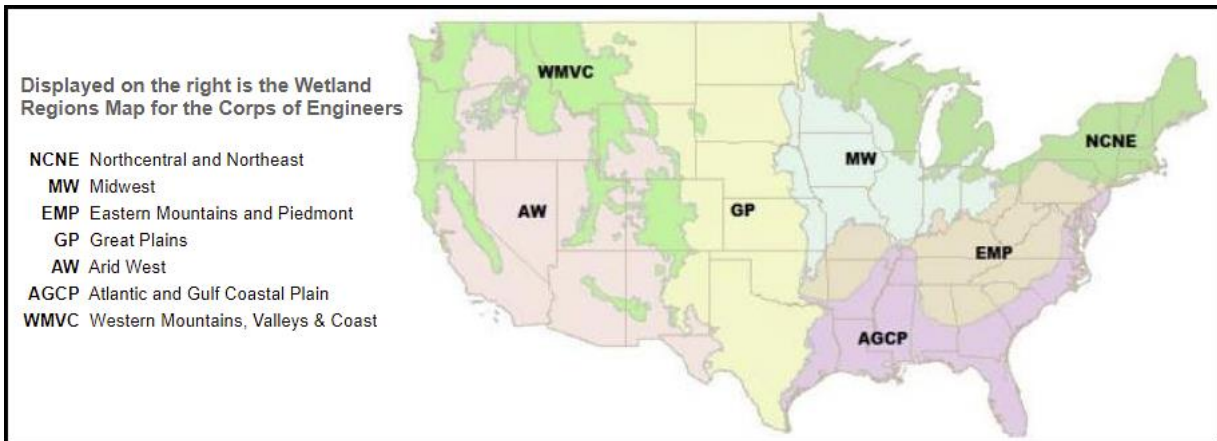


Figure 1. Mainland U. S. wetland regions, adapted from U. S. Army Corps of Engineers (2020).

## USDA Plants Code (USDA, NRCS 2023b)

SINI

## Coefficient of Conservancy (Walz et al. 2020)

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 global range of *Silene nivea* is restricted to the eastern and central United States (POWO 2023). The map in Figure 2 depicts the extent of Snowy Catchfly in North America. Morton (2020) indicated that the species was introduced in Quebec but did not persist there.

The USDA PLANTS Database (2023b) shows records of *Silene nivea* in one New Jersey county: Sussex (Figure 3). A specimen labeled as *Silene nivea* that was obtained from a site in Mercer County by Sarah Elizabeth Kandle is included in the herbarium of The College of New Jersey (Mid-Atlantic Herbaria 2023). Kandle's specimen was likely collected for a botany class that was held at the college during the 1890s (Clements 2020).

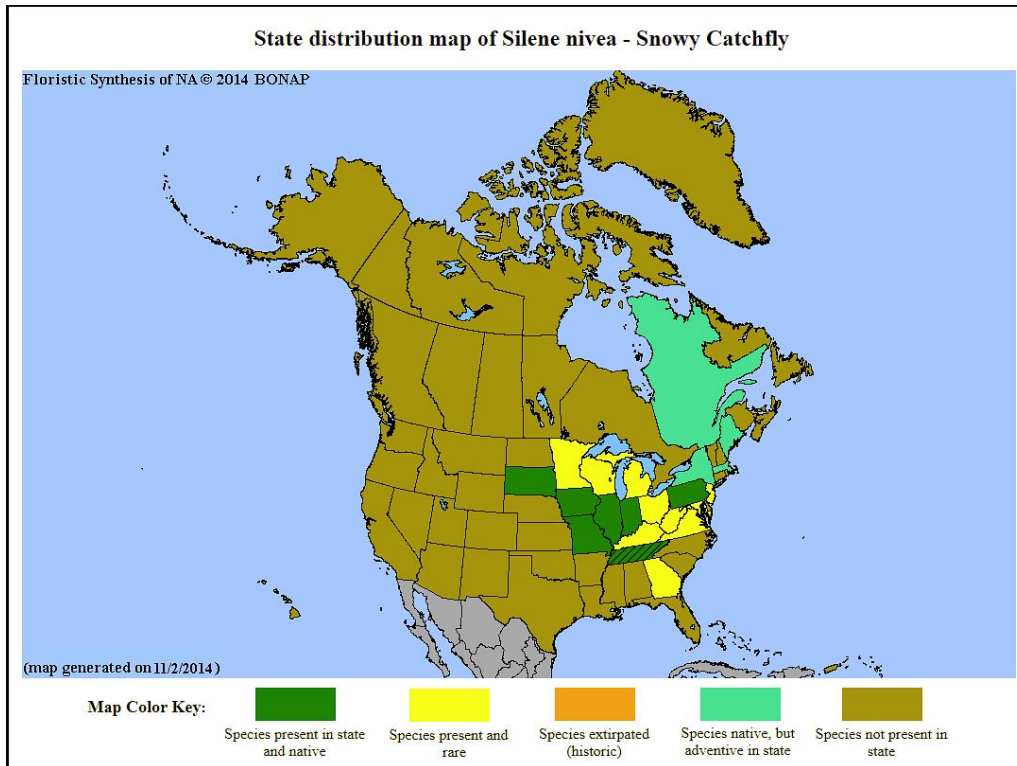


Figure 2. Distribution of *S. nivea* in North America, adapted from BONAP (Kartesz 2015). Cross hatching /// indicates a questionable presence.

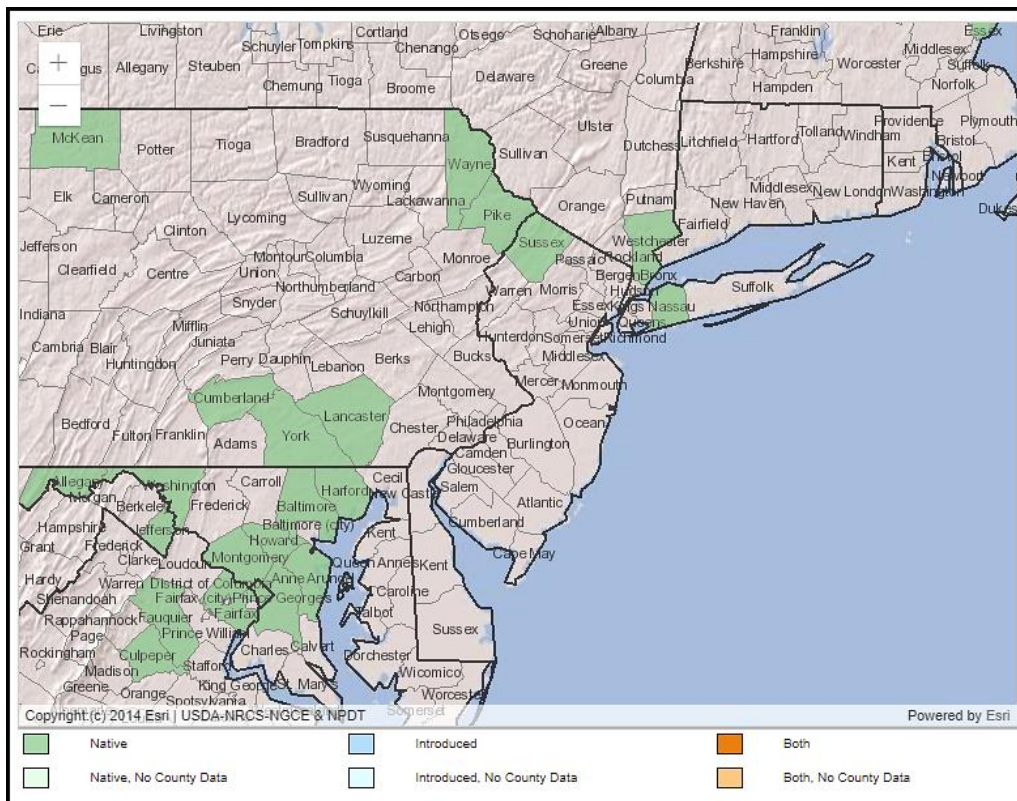


Figure 3. County records of *S. nivea* in New Jersey and vicinity (USDA NRCS 2023b).



## Conservation Status

*Silene nivea* 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. The question mark indicates that the species' status is in need of an updated review (NatureServe 2023). The map below (Figure 4) illustrates the conservation status of *S. nivea* throughout its range. The species is vulnerable (moderate risk of extinction) in three states, imperiled (high risk of extinction) in one state, critically imperiled (very high risk of extinction) in six states, and likely extirpated in the District of Columbia. In other states where Snowy Catchfly is present it is apparently secure or unranked. Occurrences in Maine are thought to be outside of the species' native range. In the North Atlantic region, which includes four Canadian provinces and twelve U. S. states, *S. nivea* was identified as a species that was likely to be a high conservation priority but was unrankable (Frances 2017).

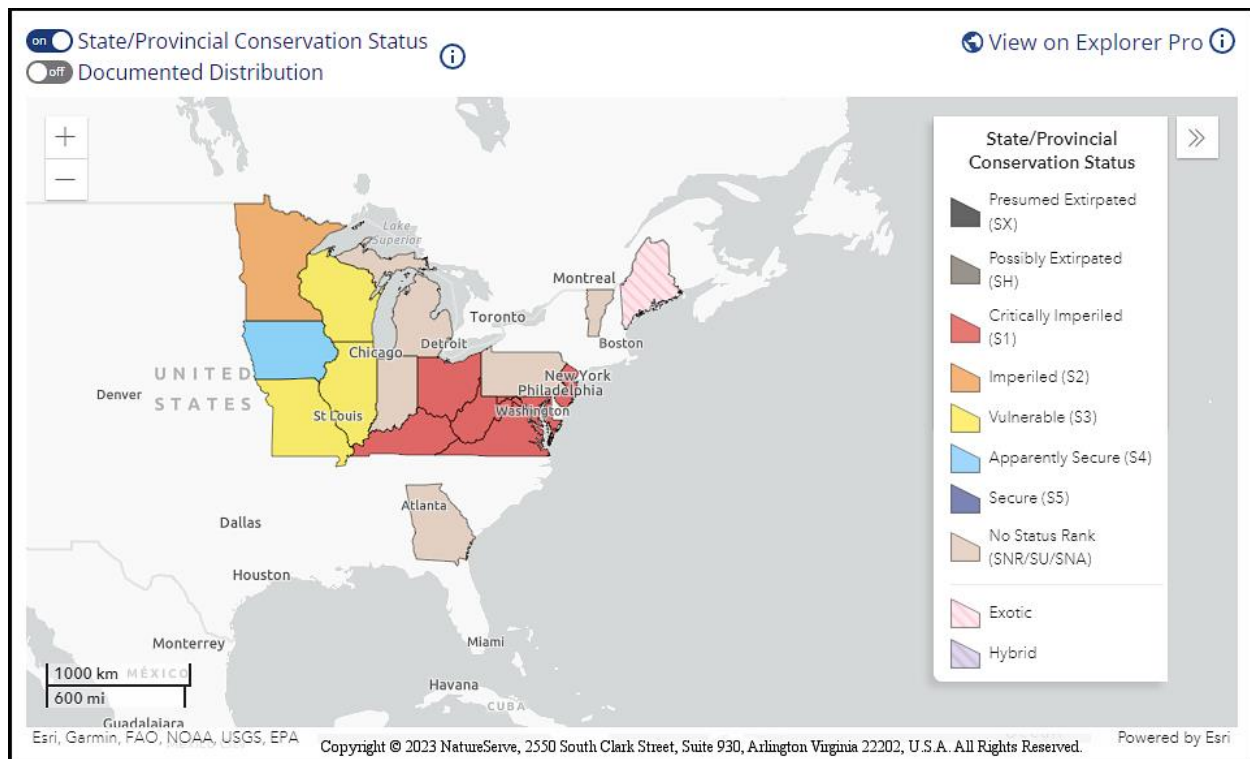


Figure 4. Conservation status of *S. nivea* in North America (NatureServe 2023).

*Silene nivea* is critically imperiled (S1) in New Jersey (NJNHP 2022). The 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. *S. nivea* 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 *S. nivea* 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).

The 1890s-era Mercer County specimen labeled as *Silene nivea* had been tucked away in a botany lab cabinet for nearly a century before the collection that included it was discovered and catalogued (Clements 2020). Consequently, when members of the Philadelphia Botanical Club discovered a population of Snowy Catchfly in 1980 it was believed to be the first record of the species in New Jersey (Abraitys 1981). Three additional populations were found during the next 15 years and all four Sussex County occurrences might still be extant, although recent searches have turned up few to no plants (NJNHP 2022).

### **Threats**

Numerous potential threats have been identified to *Silene nivea* populations throughout the species' range. Some of the most frequently cited concerns result from agricultural practices: Either direct habitat loss due to crop cultivation and grazing or habitat degradation from activities on adjacent lands that decrease water availability and introduce contaminants in surface runoff. Other reported threats include invasive flora, herbivory, and the picking of flowers (Gottlieb et al. 1994, Lynch and Weckwerth 2017, MNDNR 2023).

Nearly 80% of perennial *Silene* species are vulnerable to an anther-smut disease that is caused by *Ustilago violacea* and transmitted by insects (Altizer et al. 1998, Hood et al. 2010). However, *Silene nivea* appears to have low susceptibility to the disease, and examination of 176 herbarium specimens of *S. nivea* produced no evidence of anther smut (Gibson et al. 2010, Hood et al. 2010). *Silene* species are also susceptible to a number of rust fungi in the genus *Uromyces*, at least one of which (*U. silenes*) has been documented on *Silene nivea* (Arthur 1924). Leaf tissue damage to host plants may be primarily cosmetic but severe infections can reduce photosynthetic capacity and impair overall plant vigor (Gautam et al. 2022).

Trull and Shackelford (2018) cited successional changes in riparian habitat and competition with other plants as primary threats to *Silene nivea*. *S. nivea* itself can occasionally become weedy (Morton 2020) and under some circumstances the species has appeared to be thriving in densely vegetated sites (NJNHP 2022). Crowded growing conditions can also have the opposite effect; for example, a once large and vigorous New Jersey population was lost after the site was overrun by aggressive invasive plants such as *Artemisia vulgaris*, *Lythrum salicaria*, and *Reynoutria japonica*. Community composition may determine the outcome of competitive interactions, but additional research is needed in order to understand the critical factors that influence the relationships between *S. nivea* and other plant species.

*Silene nivea* populations in New Jersey are likely to face some level of threat from White-tailed Deer (*Odocoileus virginianus*). Deer population densities have risen considerably in the state, significantly decreasing the cover of many native herbs (Kelly 2019). *S. nivea* has no reported defenses against herbivores and other *Silene* species have been extensively browsed by deer, elk, and reindeer, typically reducing population sizes or resulting in smaller plants that flower less often (Aspi et al. 2003, Taylor et al. 2012, DiTommaso et al. 2014).

As a result of global warming, New Jersey is experiencing higher temperatures and shifting precipitation patterns which are increasing the frequency and intensity of both droughts and floods in the region (Hill 2020). The direct impacts of climactic change on *Silene nivea* plants are difficult to predict because so little is known about how environmental conditions affect the vigor or persistence of the species. However, some effects on New Jersey's populations can be projected based on their riverside locations. Bank erosion was already noted as a problem at one of the four sites, and unusually high midsummer water levels were observed at another site for three consecutive years (NJNHP 2022). Changes resulting from climate warming contribute to the probability that flooding events in the Delaware Basin will increase in both frequency and magnitude with the passage of time (Schopp and Firda 2008, UDS 2008).

### **Management Summary and Recommendations**

Three of New Jersey's four *Silene nivea* populations were once vigorous and apparently secure but all of them have declined precipitously. At one site the loss of a large population was attributed to invasive non-native plants, but at two other sites the cause of the decrease is uncertain (NJNHP 2022). More than a decade has passed since any of the occurrences were last observed, so updated surveys are needed to determine how many are still extant and assess the status of those that remain. If identification of the old Mercer County specimen can be confirmed it could point to a new location to search for the species.

*Silene nivea* is either imperiled or vulnerable in the majority of states where it occurs, so some more focused conservation efforts may be needed to preserve the species throughout its native range. Unfortunately, the lack of available information about life history strategies, community interactions, and environmental tolerances is a barrier to effective management planning for *S. nivea*. Research is needed in order to collect baseline data regarding the species' germination and establishment requirements and to determine its ranges of tolerance for temperature, light, and water availability. It would also be useful to identify pollinators and predators, evaluate self-compatibility, and study the competitive interactions between *Silene nivea* and other native and introduced plants.

### **Synonyms and Taxonomy**

The accepted botanical name of the species is *Silene nivea* (Nutt.) Muhl. ex Otth. Orthographic variants, synonyms, and common names are listed below (Morton 2020, ITIS 2023, POWO 2023, USDA NRCS 2023b). The genus *Silene* now includes species formerly assigned to separate genera such as *Lychnis*, *Melandrium*, and *Viscaria* (Morton 2020). The merge was anticipated by Barnhart (1895), who said: "*Everyone will acknowledge that the two genera Silene and Lychnis are very closely related, and that some botanist might at any time unite them. If this were done, Lychnis alba Mill (1768) would, according to the Check-List principles, become Silene alba, and Silene alba Muhl. (1813) would be relegated to the synonymy—there to remain forever—Silene nivea being substituted for it.*" Things generally unfolded as predicted for the two species in question, although the former *Lychnis/Silene alba* is now treated as either a synonym or a subspecies of *Silene latifolia* (Morton 2020, POWO 2023). Some residual

taxonomic confusion lingers from the historic application of the name *Silene alba* to two different species.

### **Botanical Synonyms**

*Cucubalus niveus* Nutt.  
*Oberna nivea* (Nutt.) Raf.  
*Silene alba* Muhl. ex Britton  
*Silene alba* Muhl. ex Rohrbach  
*Silene nivea* var. *lancifolia* Torr. & A. Gray

### **Common Names**

Snowy Catchfly  
Snowy Campion  
Evening Campion  
Notched Campion  
Western White Campion

### **References**

Abbott, J. Richard, Ralph L. Thompson, and Rudy A. Gelis. 2001. Vascular plants new to Kentucky. *SIDA, Contributions to Botany* 19(4): 1199–1202.

Abraitys, Vincent. 1981. Delaware Valley botanizing. *Bartonia* 48: 44.

Altizer, Sonia M., Peter H. Thrall, and Janis Antonovics. 1998. Vector behavior and the transmission of anther-smut infection in *Silene alba*. *The American Midland Naturalist* 139(1): 147–163.

Angelo, Ray and David E. Boufford. 2011. Atlas of the flora of New England: Caryophyllidae. *Rhodora* 113(956): 419–513.

Arthur, J. C. 1924. The Uredinales (Rusts) of Iowa. *Proceedings of the Iowa Academy of Science* 31(1): 229–255.

Aspi, Jouni, Anne Jäkäläniemi, Juha Tuomi, and Pirkko Siikamäki. 2003. Multilevel phenotypic selection on morphological characters in a metapopulation of *Silene tatarica*. *Evolution* 57(3): 509–517.

Barluenga, M., F. Austerlitz, J. A. Elzinga, S. Teixeira, J. Goudet, and G. Bernasconi. 2011. Fine-scale spatial genetic structure and gene dispersal in *Silene latifolia*. *Heredity* 106: 13–24.

Barnhart, John Hendley. 1895. The nomenclature question: Concerning homonyms. *Botanical Gazette* 20(11): 510–511.

Baskin, Carol C. and Jerry M. Baskin. 1988. Germination ecophysiology of herbaceous plant species in a temperate region. *American Journal of Botany* 75(2): 286–305.

Boerner, Ralph E. J. 1992. Plant life span and response to inoculation with vesicular-arbuscular mycorrhizal fungi. II. Species from weakly mycotrophic genera. *Mycorrhiza* 1: 163–167.

Braun, E. Lucy. 1934. The Lea Herbarium and the flora of Cincinnati. The American Midland Naturalist 15(1): 1–75.

Britton, N. L. and A. Brown. 1913. An Illustrated Flora of the Northern United States and Canada in three volumes: Volume II (Amaranth to Polypremum). Second Edition. Reissued (unabridged and unaltered) in 1970 by Dover Publications, New York, NY. 735 pp.

BugGuide. 2023. An online resource for identification, images, and information about insects, spiders and their kin in the United States and Canada. Site hosted by Iowa State University Department of Entomology. Available at <https://bugguide.net/node/view/15740>

Burleigh, J. Gordon and Timothy P. Holtsford. 2003. Molecular systematics of the eastern North American *Silene* (Caryophyllaceae): Evidence from nuclear ITS and chloroplast trnL intron sequences. Rhodora 105(921): 76–90.

Clements, Wendy L. 2020. New life for old collections. Arnoldia 78(1): 2–5.

Crandall, Raelene M. and Rebecca W. Dolan. 1997. Floristic investigation of Crooked Creek Community Juan Solomon Park, Indianapolis, Indiana. Proceedings of the Indiana Academy of Science 106: 1–23.

Deno, Norman C. 1993. Seed Germination Theory and Practice. Second Edition. Pennsylvania State University, State College, PA. 242 pp.

Deno, Norman C. 1996. First Supplement to the Second Edition of Seed Germination Theory and Practice. Self-published and distributed by the author, State College, PA. 107 pp.

DiTommaso, Antonio, Scott H. Morris, John D. Parker, Caitlin L. Cone, and Anurag A. Agrawal. 2014. Deer browsing delays succession by altering aboveground vegetation and belowground seed banks. PLoS ONE 9(3): e91155. doi:10.1371/journal.pone.0091155.

Dötterl, S., A. Jürgens, K. Seifert, T. Laube, B. Weißbecker, and S. Schütz. 2006. Nursery pollination by a moth in *Silene latifolia*: The role of odours in eliciting antennal and behavioural responses. New Phytologist 169: 707–718.

Dötterl, Stefan, Katrin Jahreiß, Umma Salma Jhumur, and Andreas Jürgens. 2012. Temporal variation of flower scent in *Silene otites* (Caryophyllaceae): a species with a mixed pollination system. Botanical Journal of the Linnean Society 169: 447–460.

Dziuk, Peter M. 2013. Photo of *Silene nivea*. Image courtesy of Minnesota Wildflowers, <https://www.minnesotawildflowers.info/flower/snowy-campion>, licensed by <https://creativecommons.org/licenses/by-nc-nd/3.0/>.

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

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>

Gautam, Ajay Kumar , Shubhi Avasthi, Rajnish Kumar Verma, Sushma, Mekala Niranjana, Bandarupalli Devadatha, Ruvishika S. Jayawardena, Nakarin Suwannarach, and Samantha C. Karunarathna. 2022. A global overview of diversity and phylogeny of the rust genus *Uromyces*. Journal of Fungi 8(6): 633, <https://doi.org/10.3390/jof8060633>

Gibson, Amanda K., Jorge I. Mena-Ali, and Michael E. Hood. 2010. Loss of pathogens in threatened plant species. Oikos 119: 1919–1928.

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.

Gottlieb, S., C. Russell, and L. Morse. 1994. *Silene nivea* conservation status factors. NatureServe, Arlington, VA. Accessed May 7, 2023 at [https://explorer.natureserve.org/Taxon/ELEMENT\\_GLOBAL.2.156625/Silene\\_nivea](https://explorer.natureserve.org/Taxon/ELEMENT_GLOBAL.2.156625/Silene_nivea)

Gross, Katherine L. 1990. A comparison of methods for estimating seed numbers in the soil. Journal of Ecology 78(4): 1079–1093.

Hartley, Thomas G. 1960. Plant communities of the LaCrosse area in western Wisconsin. Proceedings of the Iowa Academy of Science 67: 174–188.

Hill, Rebecca, Megan M. Rutkowski, Lori A. Lester, Heather Genievich, and Nicholas A. Procopio (eds.). 2020. New Jersey Scientific Report on Climate Change, Version 1.0. New Jersey Department of Environmental Protection, Trenton, NJ. 184 pp.

Hood, Michael E., Jorge I. Mena-Ali, Amanda K. Gibson, Bengt Oxelman, Tatiana Giraud, Roxana Yockteng, Mary T. K. Arroyo, Fabio Conti, Amy B. Pedersen, Pierre Gladieux and Janis Antonovics. 2010. Distribution of the anther-smut *Microbotryum* on species of the Caryophyllaceae. The New Phytologist 187(1): 217–229.

ITIS (Integrated Taxonomic Information System). Accessed May 11, 2023 at <http://www.itis.gov>

Jongejans, Eelke and Peter Schippers. 1999. Modeling seed dispersal by wind in herbaceous species. Oikos 87(2): 362–372.

- Jürgens, A., Taina Witt, and G. Gottsberger. 1996. Reproduction and pollination in central European populations of *Silene* and *Saponaria* species. *Botanica Acta* 109: 316–324.
- Jürgens, A., T. Witt, and G. Gottsberger. 2002a. Pollen grain numbers, ovule numbers and pollen-ovule ratios in Caryophylloideae: correlation with breeding system, pollination, life form, style number, and sexual system. *Sexual Plant Reproduction* 14: 279–289.
- Jürgens, A., T. Witt, and G. Gottsberger. 2002b. Flower scent composition in night-flowering *Silene* species (Caryophyllaceae). *Biochemical Systematics and Ecology* 30: 383–397.
- Jürgens, A. 2006. Comparative floral morphometrics in day-flowering, night-flowering and self-pollinated Caryophylloideae (*Agrostemma*, *Dianthus*, *Saponaria*, *Silene*, and *Vaccaria*). *Plant Systematics and Evolution* 257: 233–250.
- 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)].
- Keller, Michael and Johannes Kollmann. 1999. Effects of seed provenance on germination of herbs for agricultural compensation sites. *Agriculture, Ecosystems and Environment* 72: 87–99.
- Kelly, Jay F. 2019. Regional changes to forest understories since the mid-Twentieth Century: Effects of overabundant deer and other factors in northern New Jersey. *Forest Ecology and Management* 444: 151–162.
- Kephart, Susan, Richard J. Reynolds, Matthew T. Rutter, Charles B. Fenster, and Michele R. Dudash. 2006. Pollination and seed predation by moths on *Silene* and allied Caryophyllaceae: Evaluating a model system to study the evolution of mutualisms. *New Phytologist* 169: 667–680.
- Kost, Michael A., Dennis A. Albert, Joshua G. Cohen, Bradford S. Slaughter, Rebecca K. Schillo, Christopher R. Weber, and Kim A. Chapman. 2007. Natural Communities of Michigan: Classification and Description. Michigan Natural Features Inventory, Michigan Department of Natural Resources, Lansing, MI. 317 pp.
- Kruckeberg, A. R. 1964. Artificial crosses involving eastern North American *Silenes*. *Brittonia* 16(2): 95–105.
- Labouche, Anne-Marie and Giorgina Bernasconi. 2010. Male moths provide pollination benefits in the *Silene latifolia*–*Hadena bicurris* nursery pollination system. *Functional Ecology* 24: 534–544.
- Lammers, Thomas G. 1983. The vascular flora of Des Moines County, Iowa. *Proceedings of the Iowa Academy of Science* 90(2): 55–71.

Levine, Carol. 1995. A Guide to Wildflowers in Winter. Yale University Press, New Haven, CT. 329 pp.

Lynch, Elizabeth A. and Anna Burke Weckwerth. 2017. Herbaceous vascular flora of forested seep wetlands In Winneshiek County, Iowa, USA. Journal of the Iowa Academy of Science 124(1–4): 1–10.

Madsen, Thomas P. 2006. A Vascular Plant Inventory and Vegetation Analysis of the Johnson County Heritage Trust's Turkey Creek Preserve in Johnson County, Iowa. Prepared for the Johnson County Heritage Trust, Iowa City, IA. 52 pp.

Martineau, Nate. 2021. Three photos of *Silene nivea* from Michigan. Shared via iNaturalist at <https://www.inaturalist.org/observations/86664191>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

McAtee, W. L. 1918. A sketch of the natural history of the District of Columbia. Bulletin of the Biological Society of Washington No. 1., Washington, D. C. 142 pp.

Mid-Atlantic Herbaria. 2023. <https://midatlanticherbaria.org/portal/index.php>. Accessed on May 8, 2023.

Milus, Susan. 2017. Flower hosts its own war of the sexes. Science News 192(1): 10.

Mitchell, Richard S. and Leonard J. Uttal. 1969. Natural hybridization in Virginia *Silene* (Caryophyllaceae). Bulletin of the Torrey Botanical Club 96(5): 544–549.

MNDNR (Minnesota Department of Natural Resources). 2023. *Silene nivea* species profile Accessed May 11, 2023 at <https://www.dnr.state.mn.us/rsg/profile.html?action=elementDetail&selectedElement=PDCAR0U120>

Montesinos, Daniel, Patricio García-Fayos, and Isabel Mateu. 2006. Conflicting selective forces underlying seed dispersal in the endangered plant *Silene diclinis*. International Journal of Plant Science 167(1): 103–110.

Morton, John K. Page updated November 5, 2020. *Silene nivea* (Nuttall) Muhlenberg ex Oth. In: Flora of North America Editorial Committee, eds. 1993+. Flora of North America North of Mexico [Online]. 22+ vols. New York and Oxford. Accessed May 7, 2023 at [http://floranorthamerica.org/Silene\\_nivea](http://floranorthamerica.org/Silene_nivea)

Murphy, Michael J. C., Loy R. Phillippe, and John E. Ebinger. 2021. Flora and vegetation composition of Spring Bay Fen Nature Preserve, Woodford County, Illinois. Transactions of the Illinois State Academy of Science 114: 47–56.

NAMPG (North American Moth Photographers Group at the Mississippi Entomological Museum, at Mississippi State University). 2023. Digital Guide to Moth Identification. Available online at <http://mothphotographersgroup.msstate.edu/>



NatureServe. 2023. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed May 7, 2023 at <https://explorer.natureserve.org/>

Nekola, Jeffrey C. 1994. The environment and vascular flora of northeastern Iowa fen communities. *Rhodora* 96(886): 121–169.

Nelson, Michael W. 2012. Notes on a recently discovered population of *Hadena ectypa* (Morrison, 1875) (Noctuidae: Noctuinae: Hadenini) in Massachusetts. *The Journal of the Lepidopterists' Society* 66(1): 1–10.

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](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.

Nuttall, Thomas. 1818. The genera of North American plants and a catalogue of the species to the year 1817. Volume I. D. Heartt, Philadelphia, PA. 312 pp.

Pettersson, M. W. 1991. Pollination by a guild of fluctuating moth populations: Option for unspecialization in *Silene vulgaris*. *Journal of Ecology* 79(3): 591–604.

Popp, Magnus and Bengt Oxelman. 2007. Origin and evolution of North American polyploid *Silene* (Caryophyllaceae). *American Journal of Botany* 94(3): 330–349.

POWO. 2023. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed May 7, 2023 at <http://www.plantsoftheworldonline.org/>

Reynolds, Richard J., M. Jody Westbrook, Alexandra S. Rohde, Julie M. Cridland, Charles B. Fenster, and Michele R. Dudash. 2009. Pollinator specialization and pollination syndromes of three related North American *Silene*. *Ecology* 90(8): 2077–2087.

Rhoads, Ann Fowler and Timothy A. Block. 2007. *The Plants of Pennsylvania*. University of Pennsylvania Press, Philadelphia, PA. 1042 pp.

Robertson, Charles. 1929. *Flowers and Insects: Lists of Visitors of Four Hundred and Fifty-three Flowers*. Science Press Printing Company, Lancaster, PA. 221 pp.

Ruch, Donald G., Byron G. Torke, Kemuel S. Badger, Benjamin R. Hess, Brook N. Christian, and Paul E. Rothrock. 2008. The vascular flora and vegetational communities of Lick Creek Summit Nature Preserve in Wayne County, Indiana. *Proceedings of the Indiana Academy of Science* 117(1): 29–54.

- Ruch, Donald G., Byron G. Torke, Kemuel S. Badger, John E. Taylor, Benjamin R. Hess, and Paul E. Rothrock. 2013. The vascular flora and vegetational communities of Cabin Creek Raised Bog, Randolph County, Indiana. *Castanea* 78(4): 290–311.
- Ruch, Donald G., Kemuel S. Badger, John E. Taylor, Megan E. Smith, and Samantha Bell. 2015. The vascular flora and plant communities of Holthouse Woods Nature Preserve in Wayne County, Indiana. *Proceedings of the Indiana Academy of Science* 124(2): 106–123.
- Schopp, Robert D. and Gary D. Firda. 2008. Flood Magnitude and Frequency of the Delaware River in New Jersey, New York, and Pennsylvania. U. S. Geological Survey Open-File Report 2008-1203. 7 pp.
- Schweitzer, Dale F., Marc C. Minno, and David L. Wagner. 2018. Rare, Declining, and Poorly Known Butterflies and Moths (Lepidoptera) of Forests and Woodlands in the Eastern United States. 2nd edition. USDA Forest Health & Applied Sciences Team FHTET-2011-01. 517 pp.
- Scott, Richard K. 2009. The vascular flora of Turkey Run State Park, Parke County, Indiana. *Proceedings of the Indiana Academy of Science* 118(1): 55–75.
- Stebbins, G. Ledyard. 1970. Adaptive radiation of reproductive characteristics in angiosperms, I: Pollination mechanisms. *Annual Review of Ecology and Systematics* 1: 307–326.
- Stubbs, C. S., H. A. Jacobson, E. A. Osgood, and F. A. Drummond. 1992. Alternative forage plants for native (wild) bees associated with lowbush blueberry, *Vaccinium* spp., in Maine. Maine Agricultural Experiment Station, Technical Bulletin 148, University of Maine, Orono, ME. 54 pp.
- Taylor, R. V., J. Dingeldein, and H. Schmalz. 2012. Demography, Phenology, and Factors Influencing Reproduction of the Rare Wildflower Spalding's Catchfly (*Silene spaldingii*) on the Zumwalt Prairie. The Nature Conservancy, Enterprise, OR. 21 pp.
- Thompson, Jimmie D. 2010. The vascular flora of Boone County, Iowa (2005-2008). *Journal of the Iowa Academy of Science* 117(1–4): 9–46.
- Trull, Susan J. and Ian K. Shackleford. 2018. Regional Forester's Sensitive Plants of the Ottawa National Forest. Prepared for United States Department of Agriculture Forest Service, Ottawa National Forest, MI. 61 pp.
- UDS (City Planning 702 Urban Design Studio at the University of Pennsylvania). 2008. Climate Change: Impacts and Responses in the Delaware River Basin. Prepared for the Delaware River Basin Commission. 231 pp.
- 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](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). 2023a. *Silene nivea* 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. *Note: On the website the illustration was associated with another species (S. latifolia ssp. alba, aka S. alba) but the original source (Britton and Brown 1913) applied it to the taxon now recognized as S. nivea.*

USDA, NRCS (U. S. Dept. of Agriculture, Natural Resources Conservation Service). 2023b. PLANTS profile for *Silene nivea* (Evening campion). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed May 8, 2023 at <http://plants.usda.gov>

Walz, Kathleen S., Jason L. Hafstad, Linda Kelly, and Karl Anderson. 2020. Floristic Quality Assessment Index for Vascular Plants of New Jersey: Coefficient of Conservancy (CoC) Values for Species and Genera (update to 2017 list). New Jersey Department of Environmental Protection, New Jersey Forest Service, Office of Natural Lands Management, Trenton, NJ.

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

Weakley, A. S. and Southeastern Flora Team. 2022. Flora of the Southeastern United States. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2022 pp.

Wheeler, W. A. 1902. A contribution to the knowledge of the flora of southeastern Minnesota. In Conway MacMillan (ed). *Minnesota Botanical Studies*, Vol. II. Geological and Natural History Survey of Minnesota, Minneapolis, MN.

Young, Helen J. 2002. Diurnal and nocturnal pollination of *Silene alba* (Caryophyllaceae). *American Journal of Botany* 89(3): 433–440.

Zhou, Juannan, Richard J. Reynolds, Elizabeth A. Zimmer, Michele R. Dudash, and Charles B. Fenster. 2020. Variable and sexually conflicting selection on *Silene stellata* floral traits by a putative moth pollinator selective agent. *Evolution* 74(7): 1321–1334.