

Honckenya peploides var. *robusta*

Seabeach Sandwort

Caryophyllaceae



Honckenya peploides var. *robusta* by Bob Cunningham, 2014

Honckenya peploides var. *robusta* Rare Plant Profile

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

501 E. State St.
PO Box 420
Trenton, NJ 08625-0420

Prepared by:
Jill S. Dodds
jsdodds@biostarassociates.com

July, 2024

For:
New Jersey Department of Environmental Protection
Office of Natural Lands Management
New Jersey Natural Heritage Program
natlands@dep.nj.gov

This report should be cited as follows: Dodds, Jill S. 2024. *Honckenya peploides* var. *robusta* Rare Plant Profile. New Jersey Department of Environmental Protection, State Parks, Forests & Historic Sites, Forests & Natural Lands, Office of Natural Lands Management, New Jersey Natural Heritage Program, Trenton, NJ. 19 pp.

Life History

Honckenya peploides var. *robusta* (Seabeach Sandwort) is a rhizomatous perennial herb in the Caryophyllaceae. *Honckenya* is a monophyletic genus but *H. peploides* includes four recognized varieties—var. *robusta* is the only one that occurs in the northeastern United States (Wagner 2020). *Honckenya peploides* has been characterized as a trioecious species, meaning that individual plants within a population may produce flowers that are exclusively female, exclusively male, or bisexual (Godin 2022). Early observers reported a certain amount of gender fluidity in *H. peploides*; with some populations containing only male or female plants, some also including bisexual plants, and some having more than one kind of flower present on the same plant (Warming 1886, Knuth 1898). Malling (1957) examined sex determination in *Honckenya peploides* and concluded that plants with abortive anthers were female and plants with fully developed anthers were male but the male plants were also sometimes capable of producing functional pistillate organs in some or all of their flowers.



Left: *Honckenya peploides* (no variety) Britton and Brown 1913, courtesy USDA NRCS 2024a. Right: Scan of *H. peploides* var. *robusta* specimen collected by George B. Rossbach (1967), courtesy of the George B. Rossbach Herbarium at West Virginia Wesleyan College.

Honckenya peploides spreads vegetatively, often forming large clumps or mats. Pairs of somewhat fleshy leaves are present along the simple or branched stems. The flowers are terminal or axillary and have 5(–6) ovate sepals and the same number of petals. Female flowers

have tiny (< 2 mm) white petals and 3–5 well-developed styles, and a few rudimentary stamens may be present. Male flowers typically have 10 well-developed stamens, larger (2.5–6 mm) petals, and reduced styles. Bisexual flowers resemble male flowers but also have functioning pistils with longer styles. As suggested by the varietal name, *H. peploides* var. *robusta* is stouter than other forms of the plant. The stems are usually 3–6 mm in diameter, erect or ascending, and 1.5–5 dm in length. The lanceolate-ovate leaves are 12–28 mm long, 7–15 mm wide, and evenly spaced along the stems. The floral pedicels are short (2–3 mm) compared to those of other North American varieties and the fruiting capsules are ovoid to round and fleshy. (See Fernald 1909 & 1950, Britton and Brown 1913, Gleason and Cronquist 1991, Tiner 2009, Wagner 2020).

Baillie (2012) prepared a detailed account of the seasonal changes in *Honckenya peploides* var. *robusta* following a two-year study of several Connecticut populations. Buds appeared on old branches or rhizomes during late March. New shoots emerged during April and continued to expand through May, reaching their maximum size around the end of that month. Flowering began at the end of April and peaked during early May, although some plants continued to bloom until late May. Fruiting capsules developed in June and were gone by the end of July. Early signs of senescence were detected during late summer, most plants had collapsed by October and were desiccated by November. Few signs of the plants could be seen on the surface during the winter. In other places, flowering can sometimes begin later or continue longer and fruits may still be present in August or September (Hough 1983, Tiner 2009, Wagner 2020, Weakley et al. 2024).

Pollinator Dynamics

The flowers of *Honckenya peploides* are strongly honey-scented and secrete copious amounts of nectar, both of which are likely to attract insects (Knuth 1898, Sánchez-Vilas and Retuerto 2012, Wagner 2020). The Pacific *H. peploides* var. *major*, which Fernald (1909) noted to be larger than other varieties, is generally pollinated by small bees, flies, or ants (Tsukui and Sugawara 1992) and also by bumblebees (Lelej et al. 2012). Knuth (1898) indicated that various flies had been observed on *H. peploides* flowers in northern Europe but remarked that insect visits seemed rare considering the abundant nectar produced by the plants. Only one species of marine midge was seen visiting *H. peploides* var. *diffusa* at a site in Iceland despite the presence of numerous other potential pollinators (Philipp and Adersen 2014). Baillie (2012) noted that small ants and gnats were attracted to *H. peploides* var. *robusta* flowers in Connecticut.

Knuth (1898) observed that *H. peploides* pollen often fell from the anthers onto the flowers and suggested that it might then be carried by wind to the stigmas of nearby blooms. He also thought that self-fertilization was probable, and Warming (1886) had earlier indicated that self-pollination was likely in *Honckenya*. *H. peploides* var. *diffusa* was one of the first vascular plants to colonize Surtsey, a volcanic island that formed off the coast of Iceland during the 1960s and was set aside as a reserve for scientific research. Within a relatively short period the *Honckenya* population had grown to include millions of plants. An unusually high proportion of bisexual plants had been recorded during the early years and the rapid spread of *H. peploides* around the island was attributed to their production of seeds via self-pollination (Árnason 2014,

Philipp and Adersen 2014). However, no studies of self-compatibility or self-fertilization in *H. peploides* var. *robusta* were found.

Seed Dispersal and Establishment

The seeds of *Honckenya peploides* var. *robusta* are 2–4 mm in diameter and dull red-brown in color (Wagner 2020). *Honckenya* seeds are unique within the Caryophyllaceae because they have soft, white endosperm and there is a layer of endosperm present between the embryo and the seed coat (Martin 1946). *Honckenya* capsules may contain 3–15 seeds (Wagner 2020). The capsules of flowers that are strictly pistillate usually contain a higher number of seeds than those of bisexual flowers—means from a study of *H. peploides* var. *diffusa* populations were 8.8 for pistillate plants and 4.9 for bisexual plants (Philipp and Adersen 2014).

When *Honckenya peploides* seeds are released from the capsules they initially fall to the ground beneath the parent plants. They are locally dispersed by wind, moving across the surface of the sand until they become trapped by vegetation or debris. *H. peploides* seeds are dispersed over long distances by water (Houle 1996, Sánchez-Vilas et al. 2010, Árnason 2014). Maun (2008) cited *Honckenya* as an example of a genus that was well suited for water dispersal because both its seeds and rhizome fragments could remain afloat and viable for long periods of time. Transport by ocean currents can result in the deposition of more than one propagule at the same location; for example, Philipp and Adersen (2014) observed that multiple dispersal events had taken place at their study site in Iceland. The colonization of novel sites may be initiated by strong storms and floods (Nathan 2006).

Honckenya can maintain a persistent seed bank (Houle 1996), although a germination study that included *H. peploides* var. *peploides* found that seed viability declined with age over the seven-year project period (Walmsley and Davy 1997). Walmsley and Davy reported that the germination of *Honckenya* seeds was improved by stratification at low temperatures and by light, but was inhibited by high levels of salinity. Houle (1996) observed that seedlings mainly emerged during June, but noted that recruitment from seed might be limited by high rates of seedling mortality. Mortality rates approaching 100% were documented at a Quebec site for two consecutive years, primarily because the seedlings were buried by shifting sands. The observed effects of burial were replicated in an experimental greenhouse study: Seedling survival rates declined with just 0.5 cm of added sand and no seedlings survived the addition of 1.5 cm or more (Gagné and Houle 2002).

Habitat

In New Jersey, *Honckenya peploides* var. *robusta* is typically found above the high tide line on coastal beaches (Stone 1911, Fairbrothers and Hough 1973). Harshberger (1900, 1902) described typical *Honckenya* habitat as the middle beach zone, consisting of sand flats that were always damp. Kelly (2013) noted that the species sometimes became established on the lower beaches but such populations were often short-lived due to storm surges or erosion while populations situated on the broad overwash flats of the upper beaches were more likely to persist.

Honckenya peploides var. *robusta* occurs in similar settings throughout its range. In addition to sandy flats, the plants may also grow on dunes although they are generally located within 10 meters of sea level (Hill 1996, Tiner 2009, Angelo and Boufford 2011, Lamont and Stalter 2013, Wagner 2020). During a study of dune vegetation by Sims et al. (1987) the sandwort was encountered on ridges but not in swales. Stalter et al. (1996) noted that *H. peploides* var. *robusta* plants were frequently positioned directly in front of or adjacent to ocean-facing dunes. In some places, *H. peploides* var. *robusta* grows on pebble or cobble substrates rather than sand (Puryear 2005, Young 2021). In Connecticut *H. peploides* has also been observed growing in stony crevices among large rip-rap boulders along a railroad embankment and next to support pilings under a boardwalk (Baillie 2012).

H. peploides is nearly always found in full sun (Weakley et al. 2024). High temperatures, low moisture and nutrient availability, shifting substrates, and salt spray create a very stressful environment for the plants (Sánchez-Vilas 2007). Studies of other varieties of *Honckenya peploides* have suggested that female and male plants may utilize different strategies to cope with water stress, raising the possibility that they might preferentially colonize different microsites within their habitats as a result (Sánchez-Vilas 2007, Sánchez-Vilas et al. 2012, Philipp and Adersen 2014).



H. peploides var. *robusta* growth on different substrates in Rhode Island, Doug McGrady (2022).

Because the environment utilized by *Honckenya peploides* var. *robusta* is so challenging the sites where it occurs are usually sparsely vegetated. Seabeach Sandwort is most often found sharing a habitat with American Searocket, *Cakile edulenta* ssp. *edulenta*. Other associates may include *Ammophila breviligulata*, *Atriplex* spp., *Cenchrus tribuloides*, *Euphorbia polygonifolia*, *Polygonum glaucum*, *Salsola* spp., or *Solidago sempervirens* (Harshberger 1900, 1902 & 1909, Sorrie and Dunwiddie 1996, Breden et al. 2001, Cartier et al. 2022). In the Nova Scotia coastal communities examined by Catling et al. (1984), *H. peploides* var. *robusta* was often the dominant (or sole) species growing in exposed locations on open sand and it was also present to a lesser extent in grassy areas dominated by *Ammophila breviligulata*.

Honckenya peploides often functions as a pioneer species in coastal habitats, and as it becomes established the sandwort can modify the environment in ways that make the site more accessible to other plants and animals. *Honckenya* plants in relatively undisturbed microsites can form

large tufts or clumps that trap windblown sand, creating low mounds known as embryo dunes (Harshberger 1900, Stone 1911, Catling et al. 1984, Maun 2008, Philipp and Adersen 2014). The wind-dispersed seeds of other plants can become trapped against the mounds, which then serve as safe sites for their germination and growth (Sims et al. 1987, Gagné and Houle 2001). *H. peploides* was also thought to have aided the colonization of a young volcanic island by seabirds by providing them with nesting material (Árnason 2014).

Wetland Indicator Status

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

USDA Plants Code (USDA, NRCS 2024b)

The USDA code for *Honckenya peploides* var. *robusta* is HOPER4. The USDA treats the taxon as a subspecies rather than a variety, using the code HOPER2.

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

Honckenya peploides can be found throughout the northern hemisphere but var. *robusta* is confined to the northeastern United States and eastern Canada (POWO 2024). The map in Figure 1 depicts the extent of the variety in North America.

The USDA PLANTS Database (2024b) shows records of *Honckenya peploides* var. *robusta* in four New Jersey counties: Atlantic, Cape May, Monmouth, and Ocean (Figure 2). The data accurately reflect the currently understood distribution of the species.

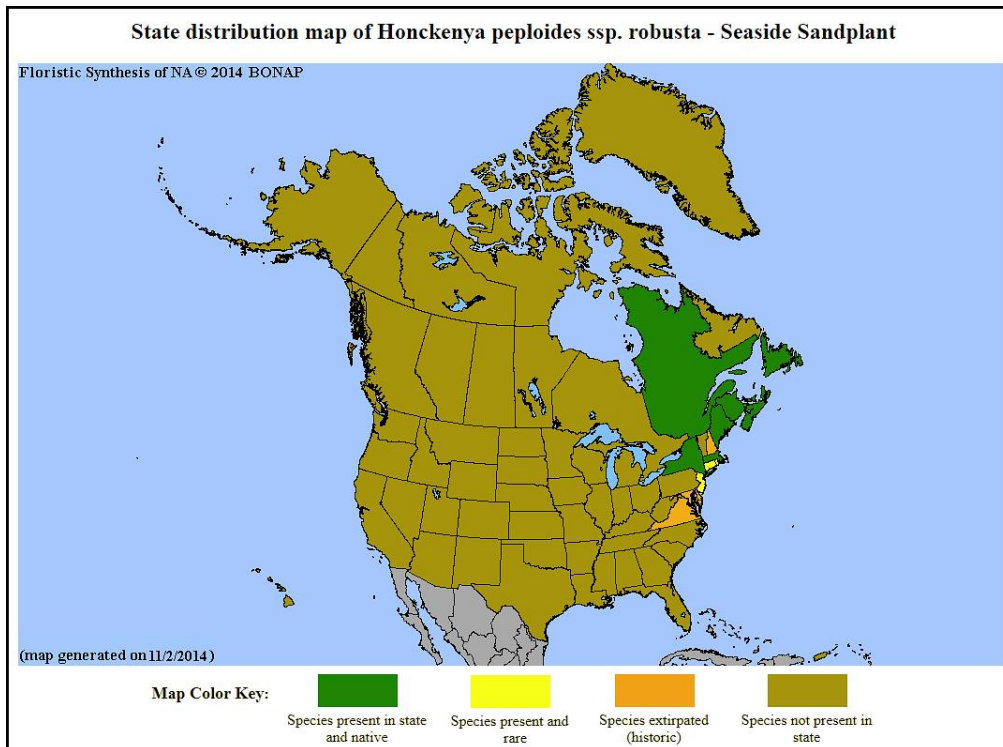


Figure 1. Distribution of *H. peploides* var. *robusta* in North America, adapted from BONAP (Kartesz 2015).

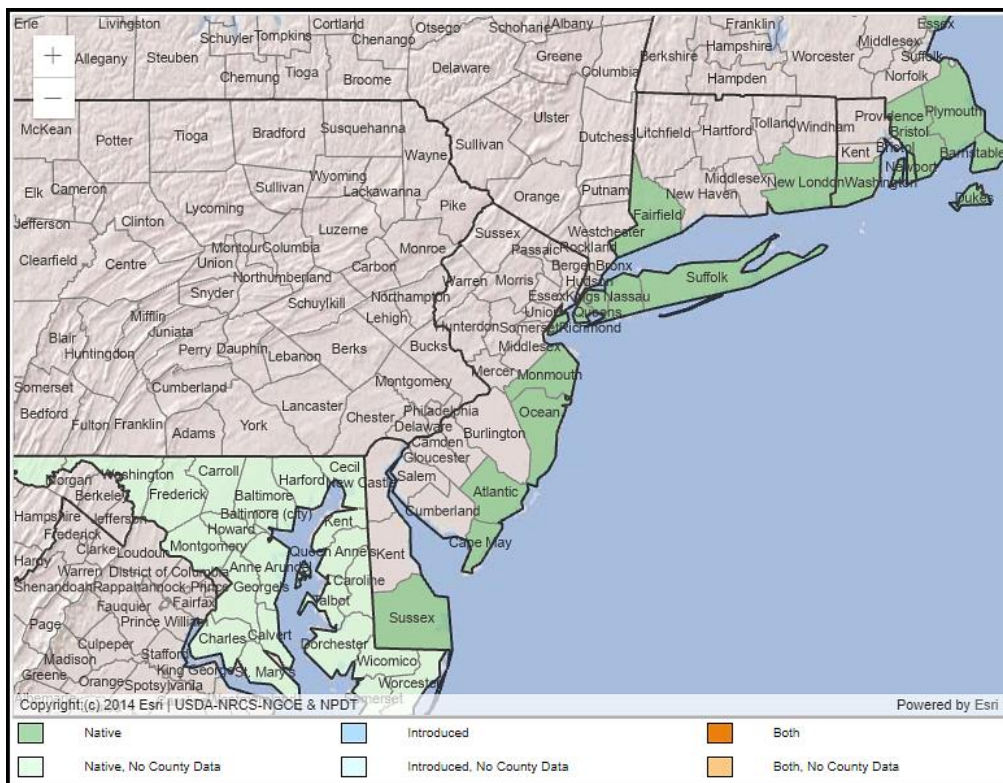


Figure 2. County records of *H. peploides* var. *robusta* in New Jersey and vicinity (USDA NRCS 2024b).

Conservation Status

Honckenya peploides var. *robusta* is considered globally secure. The G5T5 rank means that the variety has a very low risk of extinction or collapse due to a very extensive range, abundant populations or occurrences, and little to no concern from declines or threats (NatureServe 2024). The map below (Figure 3) illustrates the conservation status of *H. peploides* var. *robusta* throughout its range. The sandwort is vulnerable (moderate risk of extinction) in three provinces and one state, critically imperiled (very high risk of extinction) in one state, possibly extirpated in Delaware and Virginia, and likely extirpated in New Hampshire. Although not shown on the map, *H. peploides* is also critically imperiled in Maryland (MDNHP 2021). Hill (1996) noted that Seabeach Sandwort was declining in Connecticut, and it appears to be decreasing in frequency on some of Maine's coastal islands (Greene et al. 2005).

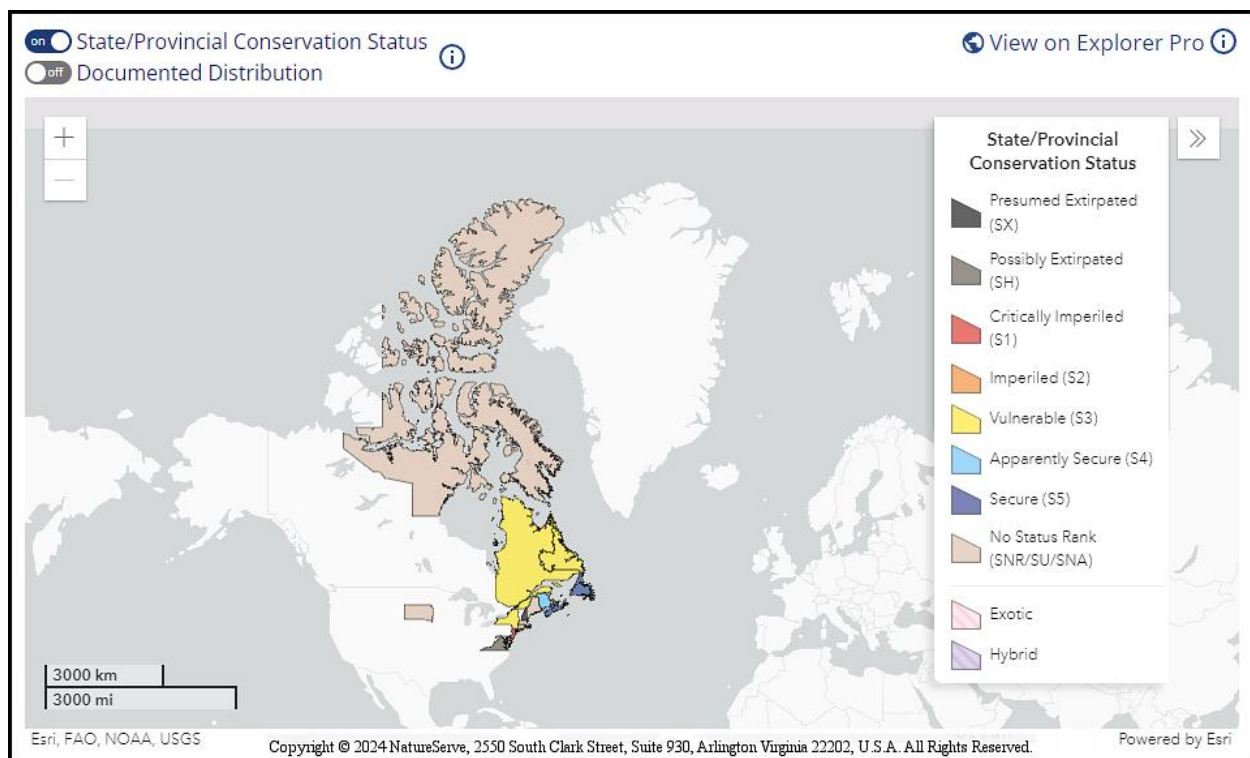


Figure 3. Conservation status of *H. peploides* var. *robusta* in North America (NatureServe 2024).

Honckenya peploides var. *robusta* is critically imperiled (S1) in New Jersey (NJNHP 2024). 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. Seabeach Sandwort 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 *H. peploides* var. *robusta* signify that the sandwort is eligible for protection under the jurisdictions of the Highlands Preservation Area (HL) and the New Jersey Pinelands (LP) (NJNHP 2010).

Honckenya peploides var. *robusta* was once fairly common on New Jersey's beaches. During the 1800s and the early part of the 1900s the species was described as "not rare" (Knieskern 1857) or "frequent" (Britton 1889) and numerous collections were made at locations all along the state's coast (Harshberger 1900 & 1902, Stone 1911, Mid-Atlantic Herbaria 2023). However, Stone (1911) observed that the sandwort appeared to be much less common than it had been in the past, noting that it had disappeared from some heavily used parts of the Jersey shore. Fairbrothers and Hough (1973) listed *Honckenya peploides* as a state endangered species because it had been rapidly disappearing, but five new occurrences were documented by David Snyder between 1980 and 2000 and other botanists relocated the species at some historical sites during the same period (Stalter and Lamont 2000, NJNHP 2024). At the turn of the century the species was listed as imperiled in New Jersey but its status was revised to critically imperiled within a decade (NJNIHP 2001, 2010). A series of coastal flora surveys conducted from 2001–2011 documented a dramatic decline in *H. peploides*. Every previously reported location along the New Jersey coast was revisited and the species was seen at less than a third of the sites where it had once occurred. No new populations were found, and both the numbers and sizes of extant populations decreased notably during the course of the decade-long study (Kelly 2013).

Threats

As previously discussed, *Honckenya peploides* grows in a highly stressful environment where few other vascular plants are able to survive. However, populations can persist for a long time when habitat conditions remain suitable. *H. peploides* var. *robusta* was consistently found at the same site in Massachusetts from 1954–2012 and at one in Nova Scotia from 1899–2002 (Stalter and Lamont 2006, 2016). Some individual *H. peploides* var. *diffusa* plants that had established on an Icelandic island during the 1970s were still present and reproducing in 2010 (Philipp and Adsersen 2014). Lucas and Freedman (1989) investigated the potential impacts of oil spills on several coastal plant communities in Nova Scotia. Aboveground parts of *Honckenya peploides* var. *robusta* were damaged or destroyed by exposure to oil but the plants readily regenerated from their rhizomes. *H. peploides* is most vulnerable during the seedling stage when the plants are small and lack a well-developed root system (Houle 1996, Gagné and Houle 2002). Nevertheless, even established populations can face an assortment of serious threats, as evidenced by the drastic decline of the species in New Jersey.

Early reported losses of *Honckenya peploides* var. *robusta* in New Jersey were mainly attributable to extensive development in the coastal region (Stone 1911, Fairbrothers and Hough 1973). Habitat degradation remains the primary threat to *H. peploides* and other rare beach plants in the state. In some cases plants have been destroyed by off-road vehicles (ORVs), beach raking, or other local maintenance activities. In other cases population losses and declines have resulted from storms that eroded beaches, shifted substrate, or deposited wrack on top of plants (Kelly 2013, 2014). Additional concerns noted for individual occurrences in the state included herbivory by rabbits and competition with *Carex kobomugi*, an introduced sedge (NJNIHP 2024).

Some comparable problems have been noted in other states. One New York population of *Honckenya peploides* var. *robusta* was lost after the site where it grew was bulldozed to create habitat for nesting terns (Coulter 1981, Stalter and Lamont 2005). *H. peploides* var. *robusta* is

also susceptible to trampling and may be eliminated by heavy foot traffic (Puryear 2005). Although an experimental study by Seer et al. (2015) reported no significant impacts on *H. peploides*, their research was conducted on a prostrate variety of the species so the results may not apply to the more upright var. *robusta*.

During the course of her life cycle study on *Honckenya peploides* var. *robusta*, Baillie (2012) encountered a population that was infected with a rust fungus. Although the rust, identified as *Uromyces acuminatus*, had not previously been documented on *Honckenya* the infection was severe and almost the entire occurrence was affected (Yun et al. 2012). Like many rust fungi, *U. acuminatus* utilizes alternate hosts during different life phases. One stage is generally restricted to *Spartina* spp. but the other can occur on an assortment of hosts in multiple plant families. The fungus causes the formation of small rust-colored pustules that become surrounded by yellow rings as cells in the adjacent tissue die. Severe infections can result in a reduction of the host's photosynthetic capacity and a consequent decrease in overall plant performance (Gautam et al. 2022).

Climate Change Vulnerability

Information from the references cited in this profile was used to evaluate the vulnerability of New Jersey's *Honckenya peploides* var. *robusta* populations to climate change. The species was assigned a rank from NatureServe's Climate Change Vulnerability Index using the associated tool (Version 3.02) to estimate its exposure, sensitivity, and adaptive capacity to changing climatic conditions in accordance with the guidelines described by Young et al. (2016) and the state climatic computations by Ring et al. (2013). Based on available data Seabeach Sandwort was assessed as Highly Vulnerable, meaning that it is likely to experience a significant decrease in abundance or range extent throughout New Jersey by 2050.

As the global climate becomes warmer both temperatures and sea levels are rising faster in New Jersey than in many other parts of the world and there is a 50% chance that sea-level rise along the state's coast will reach or exceed 0.4 meter by 2050. The higher seas are causing adjacent inland areas to flood more often and to experience elevated soil salinity. At the same time, shifting precipitation patterns are resulting in more frequent and intense storm events (Hill et al. 2020). As a beach plant, *Honckenya peploides* var. *robusta* has a high exposure to the direct impacts of sea level rise. Losses and declines due to storms and flooding have already been observed in the state (Kelly 2013, NJNHP 2024). Further damage to extant plants or potential habitat could result from strategies that are being used to prevent or mitigate the impacts of climate change such as beach fortification or replenishment. The likelihood of establishing new colonies in New Jersey is reduced by the scarcity of suitable habitat and a low probability of seedling survival. Increases in soil salinity or more frequent exposure to salt spray can inhibit seed germination, decrease seedling vigor or survival, and lower the reproductive capacity of mature plants (Walmsley and Davy 1997, Gagné and Houle 2002, Sánchez-Vilas 2007). *H. peploides* var. *robusta* is presently ranked as either critically imperiled or historical throughout the southern portion of its range so it is possible that higher temperatures have contributed to its decline.

Management Summary and Recommendations

Threats to *Honckenya peploides* var. *robusta* that arise from human activities are relatively easy to remedy by protecting the habitat. Populations of rare beach plants have been known to recover or reestablish following closure to ORV traffic or the discontinuation of raking, and some New Jersey occurrences of *H. peploides* have benefitted from fences that were erected to protect the nesting sites of rare birds or to facilitate vegetative regeneration (Kelly 2014, NJNHP 2024).

As the threats from climate change continue to mount, proactive intervention may be required in order to maintain the presence of *H. peploides* var. *robusta* in New Jersey. Kelly (2013) observed that sandwort populations were more likely to persist when they were situated in places that experienced lower levels of disturbance. Consideration should be given to focusing resources on extant occurrences in well-protected habitats or to promoting the establishment of subpopulations in sites that are sheltered from the direct impacts of storm surge and erosion.

Long-term conservation planning for Seabeach Sandwort could be aided by research. It would be useful to know whether climate has played a role in defining the southern limit of the species range. The potential for bisexual *Honckenya* flowers to develop fruit without the assistance of insects has long been inferred but no substantiating studies were found. Although some insects have been recorded visiting *H. peploides* flowers their effectiveness as pollinators has not been evaluated, and the relative importance of cross-pollination vs. self-fertilization in the production of viable seeds is unknown.

Synonyms

The accepted botanical name of the species is *Honckenya peploides* var. *robusta* (Fernald) House. The genus name has occasionally been written as *Honkenya*. Some orthographic variants, synonyms, and common names are listed below. The name *Ammodenia peploides* (L.) Rupr. was also applied to this variety by some early authors in reference to New Jersey occurrences (eg. Harshberger 1900, Stone 1911). A comprehensive review of the somewhat convoluted early taxonomic history of *H. peploides* var. *robusta* was undertaken by Moore (2002). Most contemporary taxonomists classify the plant as a subspecies rather than a variety (Kartesz 2015, Wagner 2020, ITIS 2024, POWO 2024, USDA NRCS 2024b, Weakley et al. 2024).

Botanical Synonyms

Honckenya peploides ssp. *robusta* (Fernald) Hultén
Arenaria peploides var. *robusta* Fernald
Minuartia peploides ssp. *robusta* (Fernald) Mattf.

Common Names

Seabeach Sandwort
Seaside Sandplant
Eastern Sea Sandwort

References

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

Árnason, Sigurður H. 2014. *Honckenya peploides*: Regional Gene Diversity and Global Karyotype Investigations. Master's Thesis, University of Iceland, Reykjavik. 77 pp.

Baillie, Priscilla W. 2012. Seasonal growth and development of the subarctic plant *Honckenya peploides* subsp. *robusta* (Caryophyllaceae) on Niantic Bay, Connecticut, USA. *Rhodora* 114(958): 148–162.

Breden, Thomas F., Yvette R. Alger, Kathleen Strakosch Walz, and Andrew G. Windisch. 2001. Classification of Vegetation Communities of New Jersey: Second iteration. Association for Biodiversity Information and New Jersey Natural Heritage Program, Office of Natural Lands Management, Division of Parks and Forestry, NJ Department of Environmental Protection, Trenton, NJ. 230 pp.

Britton, N. L. 1889. Catalogue of plants found in New Jersey. Geological Survey of New Jersey, Final report of the State Geologist 2: 27–642.

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.

Cartier, Isabelle, Félix Gagnon, and Luc Bouchard. 2022. Protection du littoral du chemin des wagonniers à Sept-Îles – Avis de projet. Rapport produit pour Rio Tinto – IOC. 22 pp.

Catling, P. M., B. Freedman, and Z. Lucas. 1984. The vegetation and phytogeography of Sable Island, Nova Scotia. *Proceedings of the Nova Scotian Institute of Science* 34: 181–247.

Coulter, Malcolm C. 1981. A flora of Great Gull Island, Long Island Sound, New York. *Bulletin of the Torrey Botanical Club* 108(2): 272–277.

Cunningham, Bob. 2014. Cover photo of *Honckenya peploides* var. *robusta*. Used with permission.

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.

Fernald, M. L. 1909. The variations of *Arenaria peploides* in America. *Rhodora* 11(126): 109–115.

- Fernald, M. L. 1950. Gray's Manual of Botany. Dioscorides Press, Portland, OR. 1632 pp.
- Gagné, Jean-Michel and Gilles Houle. 2001. Facilitation of *Leymus mollis* by *Honckenya peploides* on coastal dunes in subarctic Quebec, Canada. Canadian Journal of Botany 79(11): 1327–1331.
- Gagné, Jean-Michel and Gilles Houle. 2002. Factors responsible for *Honckenya peploides* (Caryophyllaceae) and *Leymus mollis* (Poaceae) spatial segregation on subarctic coastal dunes. American Journal of Botany 89(3): 479–485.
- Gautam, Ajay Kumar, Shubhi Avasthi, Rajnish Kumar Verma, Sushma, Mekala Niranjana, Bandrupalli 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>
- 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.
- Godin, V. N. 2022. Trioecy in flowering plants. Biological Sciences 507: 299–309.
- Greene, Craig W., Linda L. Gregory, Glen H. Mittelhauser, Sally C. Rooney, and Jill E. Weber. 2005. Vascular flora of the Acadia National Park region, Maine. Rhodora 107(930): 117–185.
- Harshberger, John W. 1900. An ecological study of the New Jersey strand flora. Proceedings of the Academy of Natural Sciences of Philadelphia 52: 623–671.
- Harshberger, John W. 1902. Additional observations on the strand flora of New Jersey. Proceedings of the Academy of Natural Sciences of Philadelphia 54(3): 642–669.
- Harshberger, John W. 1909. The comparative leaf structure of the strand plants of New Jersey. Proceedings of the American Philosophical Society 48(191): 72–89.
- Hill, Steven R. 1996. The flora of Latimer Point and vicinity, New London County, Connecticut. Rhodora 98(894): 180–216.
- 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.
- Hough, Mary Y. 1983. New Jersey Wild Plants. Harmony Press, Harmony, NJ. 414 pp.
- Houle, Gilles. 1996. Environmental filters and seedling recruitment on a coastal dune in subarctic Quebec (Canada). Canadian Journal of Botany 74(9): 1507–1513.

ITIS (Integrated Taxonomic Information System). Accessed July 12, 2024 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)].

Kelly, Jay F. 2013. The status and distribution of *Amaranthus pumilus* Raf. (Seabeach Amaranth) and other rare beach plant species in New Jersey: Field surveys and historical records. *Bartonia* 66: 28–60.

Kelly, Jay F. 2014. Effects of human activities (raking, scraping, off-road vehicles) and natural resource protections on the spatial distribution of beach vegetation and related shoreline features in New Jersey. *Journal of Coastal Conservation* 18: doi 10.1007/s11852-014-0324-1.

Knieskern, P. D. 1857. A Catalogue of Plants Growing Without Cultivation in the Counties of Monmouth and Ocean, New Jersey. Published at the "True American" Office, Trenton, NJ. 41 pp.

Knuth, Paul. 1898. *Handbuch der Blütenbiologie*. Vol. II. Wilhelm Engelmann, Leipzig, Germany. 705 pp.

Lamont, Eric E. and Richard Stalter. 2013. Flora of Plum Island, Suffolk County, New York. *The Journal of the Torrey Botanical Society* 140(4): 465–479.

Lelej, A., Proshchalykin, M.Y., Kupianskaya, A., Berezin, M., and Tkacheva, E.Y. 2012. Tropical links of bumble bees (Hymenoptera, Apidae: *Bombus* Latreille) on north-west Pacific islands, the Russian Far East. *Eurasian Entomological Journal* 11: 261–269.

Lucas, Z. and B. Freedman. 1989. The effects of experimental spills of natural gas condensate on three plant communities on Sable Island, Nova Scotia, Canada. *Oil and Chemical Pollution* 5(4): 263–272.

Malling, Heinrich 1957. The chromosome number of *Honckenya peploides* (L.) Ehrh., with a note on its mode of sex determination. *Hereditas* 43: 517–524.

Martin, A. C. 1946. The comparative internal morphology of seeds. *The American Midland Naturalist* 36(3): 513–660.

Maun, M. A. 2008. Burial of plants as a selective force in sand dunes. *In* M. L. Martínez and N. P. Psuty (eds.), *Coastal Dunes: Ecology and Conservation*. Ecological Studies, Vol. 171, Springer-Verlag, NY.

McGrady, Doug. 2022. Two photos of *Honckenya peploides* var. *robusta* from Rhode Island. Shared via iNaturalist at <https://www.inaturalist.org/observations/145730789> and

<https://www.inaturalist.org/observations/145099950>, licensed by <https://creativecommons.org/licenses/by-nc/4.0/>

MDNHP (Maryland Natural Heritage Program). 2021. List of Rare, Threatened, and Endangered Plants of Maryland. Maryland Department of Natural Resources, Annapolis, MD. Accessed July 16, 2024 at https://dnr.maryland.gov/wildlife/Pages/plants_wildlife/rte/rteplants.aspx

Mid-Atlantic Herbaria. 2023. Accessed at <https://midatlanticherbaria.org/portal/index.php> on May 14, 2023.

Moore, Gerry. 2002. A review of the nomenclature in Witmer Stone's "The Plants of Southern New Jersey". *Bartonia* 61: 27–47.

Nathan, Ran, Frank M. Schurr, Orr Spiegel, Ofer Steinitz, Ana Trakhtenbrot, and Asaf Tsoar. 2008. Mechanisms of long-distance seed dispersal. *Trends in Ecology and Evolution* 23(11): 638–647.

NatureServe. 2024. NatureServe Explorer [web application]. NatureServe, Arlington, VA. Accessed July 12, 2024 at <https://explorer.natureserve.org/>

NJNHP (New Jersey Natural Heritage Program). 2010. Explanation of Codes Used in Natural Heritage Reports. Updated March 2010. Available at https://nj.gov/dep/parksandforests/natural/docs/nhpcodes_2010.pdf

NJNHP (New Jersey Natural Heritage Program). 2001 & 2010. Lists of Endangered Plant Species and Plant Species of Concern, dated September 2001 and January 2010, respectively. Biotics Database. NatureServe, Arlington, VA.

NJNHP (New Jersey Natural Heritage Program). 2024. Biotics 5 Database. NatureServe, Arlington, VA. Accessed March 15, 2024.

Philipp, M. and H. Adersen. 2014. Colonization of an empty island: How does a plant with a plastic gender system respond? *Biogeosciences* 11: 6657–6665.

POWO. 2024. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Accessed July 12, 2024 at <http://www.plantsoftheworldonline.org/>

Puryear, Kristen. 2005. Ecological and Land Management Survey of Napatree Beach and Napatree Point, Westerly, Rhode Island. Report prepared for Rhode Island Natural History Survey, Kingston, RI. 57 pp.

Ring, Richard M., Elizabeth A. Spencer, and Kathleen Strakosch Walz. 2013. Vulnerability of 70 Plant Species of Greatest Conservation Need to Climate Change in New Jersey. New York Natural Heritage Program, Albany, NY and New Jersey Natural Heritage Program, Department

of Environmental Protection, Office of Natural Lands Management, Trenton, NJ, for NatureServe #DDCF-0F-001a, Arlington, VA. 38 pp.

Rossbach, George B. 1967. Specimen of *Honckenya peploides* var. *robusta* collected in Maine on August 17, 1967. Public domain image of herbarium sheet courtesy of West Virginia Wesleyan College, George B. Rossbach Herbarium via MidAtlantic Herbaria. Accessed July 12, 2024 at <https://midatlanticherbaria.org/portal/index.php>. Image modified to remove location.

Sánchez-Vilas, Julia. 2007. Sexual Dimorphism in Ecological and Physiological Traits of the Subdioecious Dune Plant *Honckenya peploides* (L.) Ehrh. Doctoral Dissertation, Universidade de Santiago de Compostela, Santiago, Spain. 233 pp.

Sánchez-Vilas, Julia and Rubén Retuerto. 2012. Response of the sexes of the subdioecious plant *Honckenya peploides* to nutrients under different salt spray conditions. *Ecological Research* 27: 163-171.

Sánchez-Vilas, J., M. Philipp, and R. Retuerto. 2010. Unexpectedly high genetic variation in large unisexual clumps of the subdioecious plant *Honckenya peploides* (Caryophyllaceae). *Plant Biology* 12: 518–525.

Sánchez-Vilas, Julia, Raimundo Bermúdez, and Rubén Retuerto. 2012. Soil water content and patterns of allocation to below- and above-ground biomass in the sexes of the subdioecious plant *Honckenya peploides*. *Annals of Botany* 110: 839–848.

Seer, Franziska K., Ulrich Irmeler, and Joachim Schrautzer. 2015. Effects of trampling on beach plants at the Baltic Sea. *Folia Geobotanica* 50: 303–315.

Sims, R. A., G. M. Wickware, and D. W. Cowell. 1987. A study of coastal vegetation at a site on Hudson Bay near Winisk, Ontario. *The Canadian Field-Naturalist* 101(3): 335–345.

Sorrie, Bruce A. and Peter W. Dunwiddie. 1996. The Vascular and Non-vascular Flora of Nantucket, Tuckernuck, and Muskeget Islands. A joint publication by the Massachusetts, Audubon Society, Massachusetts Natural Heritage and Endangered Species Program, Nantucket Maria Mitchell Association, and The Nature Conservancy, Nantucket, MA. 145 pp.

Stalter, Richard and Eric E. Lamont. 2000. Vascular flora of Sandy Hook, New Jersey. *Bartonia* 60: 105–116.

Stalter, Richard and Eric E. Lamont. 2005. The historical and extant flora of Great Gull Island, New York. *The Journal of the Torrey Botanical Society* 132(4): 628–634.

Stalter, Richard and Eric E. Lamont. 2006. The historical and extant flora of Sable Island, Nova Scotia, Canada. *The Journal of the Torrey Botanical Society* 133(2): 362–374.

Stalter, Richard and Eric E. Lamont. 2016. Changes in the vascular plant diversity of the Monomoy Islands, Massachusetts. *Rhodora* 118(973): 86–106.

Stalter, Richard, Michael D. Byer, and John T. Tanacredi. 1996. Rare and endangered plants at Gateway National Recreation Area: A case for protection of urban natural areas. *Landscape and Urban Planning* 35(1): 41–51.

Stone, Witmer. 1911. *The Plants of Southern New Jersey*. Quarterman Publications, Boston, MA. 828 pp.

Tiner, Ralph W. 2009. *Field Guide to Tidal Wetland Plants of the Northeastern United States and Neighboring Canada*. University of Massachusetts Press, Amherst, MA. 459 pp.

Tsukui, T. and T. Sugawara. 1992. Dioecy in *Honkenya peploides* var. *major* (Caryophyllaceae). *The Botanical Magazine, Tokyo* 105: 615–624.

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). 2024a. *Honkenya peploides* 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). 2024b. PLANTS profile for *Honkenya peploides* ssp. *robusta* (Seaside Sandplant). The PLANTS Database, National Plant Data Team, Greensboro, NC. Accessed July 12, 2024 at <http://plants.usda.gov>

Wagner, Warren L. Page updated November 5, 2020. *Honkenya peploides* subsp. *robusta* (Fernald) Hultén. 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 12, 2024 at [http://floranorthamerica.org/Honkenya peploides subsp. robusta](http://floranorthamerica.org/Honkenya_peploides_subsp._robusta)

Walmsley, C. A. and A. J. Davy. 1997. Germination characteristics of shingle beach species, effects of seed ageing and their implications for vegetation restoration. *Journal of Applied Ecology* 34(1): 131–142.

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.

Warming, M. E. 1886. Sur la structure et le procédé présumé de pollination chez quelques fleurs groenlandaises. *Bulletin de l'Académie royale des sciences et des lettres de Danemark*: 25–33.

Weakley, A. S. and Southeastern Flora Team. 2024. Flora of the Southeastern United States. Edition of March 4, 2024. University of North Carolina Herbarium, North Carolina Botanical Garden, Chapel Hill, NC. 2023 pp.

Young, Steve. 2021. A new rare plant survey for Fishers Island, New York. Long Island Botanical Society Newsletter 31(4): 29–35.

Young, Bruce E., Elizabeth Byers, Geoff Hammerson, Anne Frances, Leah Oliver, and Amanda Treher. 2016. Guidelines for Using the NatureServe Climate Change Vulnerability Index, Release 3.02, 1 June 2016. NatureServe, Arlington, VA. 65 pp.

Yun, H. Y., A. M. Minnis, L. J. Dixon, L. A. Castlebury, and S. M. Douglas. 2010. First report of *Uromyces acuminatus* on *Honckenya peploides*, the endangered Seabeach Sandwort. Plant Disease 94(2): 279.