

# Scientific Note: Here the Whole Time: A Revised Understanding of White Alumroot (*Heuchera alba*, Saxifragaceae) in the Susquehanna River Valley

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## ABSTRACT

*Heuchera alba* and *H. pubescens* (Saxifragaceae) are closely related species of alumroot endemic to the Appalachian region of eastern North America that can be difficult to distinguish morphologically. *Heuchera pubescens* has been understood to occupy a range from Kentucky to Pennsylvania, with the distribution of *H. alba* restricted to Virginia and West Virginia—plus a recently-recorded extension into Pennsylvania discovered with the help of social media. The uncovering of *H. alba* in Pennsylvania has challenged historical perceptions of *Heuchera* distributions in the state, particularly as this relates to the current concept of *H. pubescens* which may be in need of revision. The present survey of *Heuchera* conducted in Susquehanna River Valley finds that all previous records of *H. pubescens* in the valley are instead attributable to *H. alba*. Additionally, collections of pollinators at these sites beginning in 2019 established the frequent presence of a specialized pollinator, the alumroot cellophane bee (*Colletes aestivalis*)—the first state record of this bee in Pennsylvania in over a century. Possible reliance of a network of disjunct plant populations in narrowly-defined habitats on an oligolectic bee for pollination services suggests that assessing the population genetics of *H. alba* in Pennsylvania is an important future step.

**Key words:** *Colletes*, *Heuchera*, conservation, pollination, Pennsylvania

## INTRODUCTION

*Heuchera* (Saxifragaceae) is a genus comprising approximately 45 species (Folk and Weakley, 2022; Pantinople et al. 2024) all endemic to North America, some of which can be difficult to differentiate morphologically (Wells and Shipes 2009). Similarities among species are partly attributable to sympatric and allopatric hybridization between species (Folk et al. 2017, 2023), which has caused confusion in defining boundaries relating to taxonomy (Wells 1984). This uncertainty has led to challenges in definitively identifying and circumscribing distributions of several of the ~17 taxa (as per Folk and Weakley 2022) encountered in eastern North America.

Two *Heuchera* species have been historically recognized as occurring in the state of Pennsylvania (Rhoads and Block 2007): *H. americana* L. and *H. pubescens* Pursh. However, a third species, previously unrecorded in the state, was identified in 2017 during a survey of vegetation on a cliffside

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above the Susquehanna River in the Overlook Section of Shikellamy State Park, Selinsgrove, Pennsylvania (Schuette et al. 2018; Martine et al. 2018). Through social media (Martine 2017), the identification of the plant was determined by R. Folk to be the globally-imperiled (G2) *Heuchera alba* Rydb., known as white alumroot (Figure 1)—a species previously only known from Virginia and West Virginia.

*Heuchera alba* was described by Rydberg from collections made on the northeast slope of Snowy Mountain, West Virginia, in 1925 (Rydberg 1926). Although suggested as being closely allied with *H. scabra* Rydb. (now *H. longiflora* Rydb.) (Rydberg 1926), recent morphological and molecular analyses of *Heuchera* (Folk and Freudenstein 2014; Folk et al. 2017) support a sister relationship with *H. pubescens*. Current understanding of these two sister taxa suggests that *H. pubescens* is more common and more globally secure (G4); and herbarium records suggest that there are states where the two species co-occur (PA, WV, VA), although efforts to better understand the morphological differences between the species (see Schuette et al. 2018) may lead to greater confidence in these identifications.

Immediately following the identification of *Heuchera alba* at Shikellamy Bluffs, seven more Pennsylvania populations were subsequently recorded in both the Susquehanna and Juniata River Valleys (Schuette et al. 2018) in habitats typically described as sustaining populations of *H. pubescens*—raising further questions about the veracity of *H. pubescens* records in the state. Based on the number of known *H. alba* populations, the number of individuals recorded (~1000, in total), and the amount of unexplored appropriate habitat, Schuette et al. (2018) recommended a Pennsylvania state rank of critically imperiled to imperiled (S1S2).

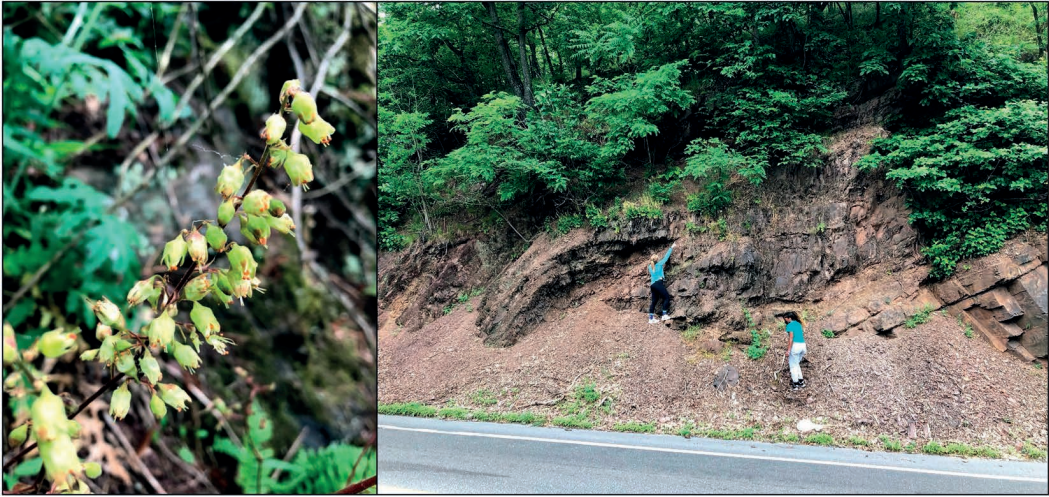
We here describe the results of an additional and rigorous survey of Susquehanna River Valley cliffside habitats in Pennsylvania to determine the identity and abundance of *Heuchera* populations in the region. Following the observation of cellophane bees (*Colletes*) at the Shikellamy Bluffs site, collections of bees were made when seen actively foraging on flowers during the survey to establish whether these were *C. aestivalis* (alumroot cellophane bee, not seen in Pennsylvania since the early 1900s).

## MATERIALS AND METHODS

Surveys (Figure 1) were conducted by AB, MW, SS, and CM in more than 30 sites in the Susquehanna River Valley during June and July of 2021 (see Avril 2021), including sites along both the North and West branches of the Susquehanna River) with additional surveys done by CM through March 2025. Survey sites were initially chosen based on herbarium records of *Heuchera pubescens* in the region, with additional sites searched when appropriate habitat was assumed to be present. Species identifications were based on the diagnostic characters described and shown (photos and illustrations) in Schuette et al. (2018), with particular attention to floral characters such as the degree of hypanthium zygomorphy (which is most pronounced in *H. alba*). At each of the sites, a voucher specimen of *Heuchera* was collected (along with specimens of associated plant species) and deposited in the Manning Herbarium at Bucknell University (BUPL). At six of the sites, seven bee specimens were also collected and sent to entomologists Mike Slater and Sam Droege for identification, although bees were observed at more than six sites. Approximately 1–2 hours were spent surveying the plants at each site, noting the abundance of *Heuchera* and observing floral visitors. At each of the sites where *Heuchera* was present, 10 leaves were collected from 10 different plants as a population sample and samples were placed in a bag of silica to dry them out to be used for DNA extraction at a later date (Folk et al. in prep.).

## RESULTS AND DISCUSSION

*Heuchera alba* is far more abundant in the Susquehanna River Valley than previously reported by Schuette et al. (2018). Every population we visited that was associated with a herbarium record for *H. pubescens* was morphologically found to represent *H. alba* following criteria laid out by Schuette

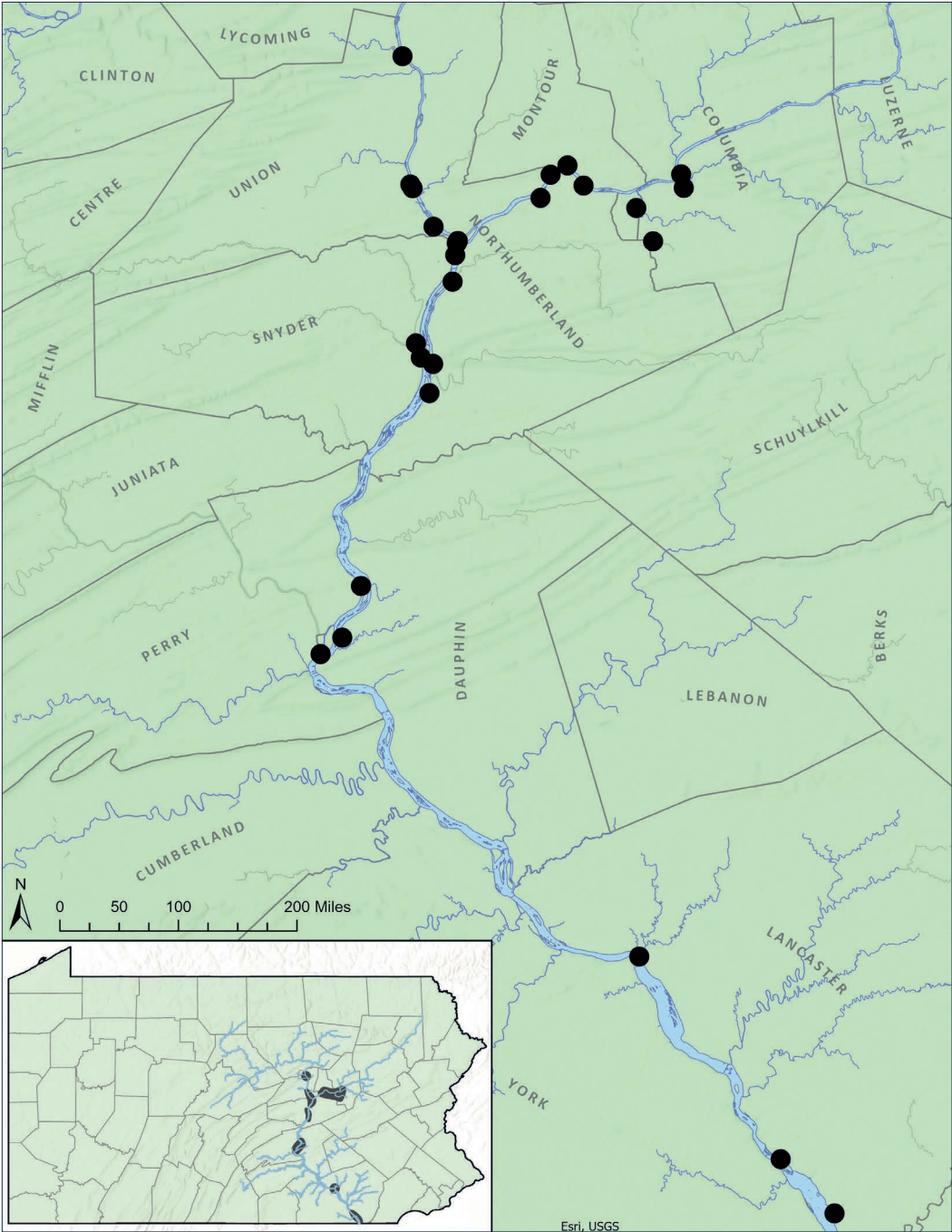


**Figure 1.** *Heuchera alba* (white alumroot, Saxifragaceae) flowers and habitat: (left) *H. alba* inflorescence; (right) M. Wickers and A. Barnes working in one of ca. 30 Susquehanna River Valley populations of *H. alba* surveyed for this study.

et al. (2018). Our surveys found that populations of *H. alba* consist of anywhere from 8–10 to ca. 1000 individuals, most of these being mature plants given little observed seedling recruitment. The distribution range of *H. alba* within the Susquehanna River Valley extends from Lancaster County to northern Union County (Figure 2), the northernmost recorded population consisting of about 30 plants on a cliff face overhanging Rt. 15 in New Columbia. Numerous similarly steep and rocky sites were visited north of this locality in both Lycoming and Clinton counties, with no populations of *Heuchera* (any species) located. The drop-off in *H. alba* occurrences appears to be related to the geographic limits of acidic sandstone geologies in the region. Bees collected in six of the sites, two male and five female, were identified by Mike Slater and Sam Droege as *Colletes aestivalis*, the alumroot cellophane bee.

Surveys throughout the Susquehanna River Valley have now provided evidence, as suggested by Schuette et al. (2018), that the distribution of *Heuchera alba* extends well beyond the historically-recognized range consisting only of the Appalachian ridges of Virginia and West Virginia. Observations by SS suggest the species is also locally abundant in appropriate habitats of Pennsylvania's Juniata River and Youghiogheny River Valleys in the south central and southwestern parts of the state respectively. The revised understanding of *H. alba* in Pennsylvania, where the species appears to be more abundant than anywhere else in its natural range, may have implications for the recognized conservation status of *H. alba* in both Pennsylvania (suggested S1S2, critically imperiled/imperiled) and globally (currently G2, imperiled). In West Virginia, additional locality records of *H. alba* have led to a revision of its state conservation status to S3 (vulnerable). The current understanding of *Heuchera* in Pennsylvania also requires revision given that sites previously attributed to *H. pubescens* (based on herbarium records) were found to instead be sites for *H. alba*, suggesting that *H. pubescens* is not actually present in the state, which may lead to status review for this species as well. As such, the flora of Pennsylvania appears to include just two native *Heuchera* species: *H. alba* and *H. americana*. Efforts employing molecular data to estimate the true ranges of *H. alba* and *H. pubescens* in the Appalachians, as well as their ostensible hybridization, are currently underway (Folk et al. in prep.).

The establishment of a northern range limit for the species (northern Union County, Pennsylvania) allows for consideration of threats to populations on the range edge. Range edge populations are often small (and thus potentially inbreeding), but also tend to harbor genotypes that may not be present in the central range of a species due to local adaptation to conditions that are more dynamic than



**Figure 2.** Map illustrating geographic extent of *Heuchera alba* (white alumroot, Saxifragaceae) in the Susquehanna River Valley of Pennsylvania based on surveys conducted between 2021–2025. Note that the West Branch Susquehanna River flows through Union County, meeting the North Branch Susquehanna River (here shown flowing through Columbia and Montour counties) at the northern shared border of Snyder and Northumberland counties to form the main stem Susquehanna. Map by Rebecca Beneroff.

what a species faces in the core of its distribution (see Hampe and Petit 2005; Rehm et al. 2015). Range edge populations in *Heuchera* also tend to have very few floral visitors and low fruit set (RAF pers. obs.), suggesting that prevalent pollinator limitation as well as abiotic factors set range limits. Because of this, range edge populations are important conservation targets when considering how a species might rapidly respond and migrate during oscillations in climate—and because they represent plant survival at abiotic and biotic extrema they can be critical for the preservation of genotypes that might help a species adapt not just at a leading edge but across its distribution (e.g. Cook 1961). Pennsylvania is home to several Central Appalachian endemics with a northern range edge that occurs in the state (see McDonnell et al. 2021; Buabeng 2024; Moore et al. 2025; Zizis 2025) and the conservation management of these species is a key priority.

The northernmost *Heuchera alba* population we recorded (New Columbia) appears to be rather stable (ca. 30 plants) but it is on a narrow outcrop between a shale mine and a road, and thus subject to incursions of weedy species coming from both sources. Despite much searching in similar (though highly-disturbed) habitats with similar geology, the next-nearest population we encountered was 10 miles south, a small group of fewer than 10 plants hanging over the West Branch Susquehanna River bank near the Bucknell University campus. This is followed by a long-known *Heuchera* site at “Gundy’s Farm” (with herbarium collections dating to the early 1900s) where only about a dozen plants are holding on. In each of these sites the small area of open cliff face is heavily invaded with *Celastrus orbiculatus* Thunb., *Lonicera japonica* Thunb., *Lonicera maackii* (Rupr.) Herder, *Alliaria petiolata* (M. Bieberstein) Cavara & Grande, *Chelidonium majus* L., *Hypericum perforatum* L., *Microstegium vimineum* (Trinius) A. Camus and other exotic taxa. *Heuchera alba* can be found in similarly small and invaded populations scattered from Gundy’s Farm to 10 miles south at Shikellamy Bluffs, where more than 1000 plants are present on cliffs as tall as 350 feet. Given the potential genotypic diversity represented among the small northern populations, and the likely status of *Heuchera* as a poor competitor, we suggest that active removal and continued management of invasive plants at these sites be prioritized. The apparently low recruitment of seedlings at our study sites is a phenomenon deserving of further study; it is unclear whether this is related to competition, herbivory (none directly witnessed), or other challenges—or whether recruitment in the steep cliffside habitats is highly episodic and has just not been recorded during our surveys. Dehisced fruits of pressed and dried voucher specimens frequently shed a great deal of seed, suggesting that seed viability tests could be a future option.

Geographic isolation coupled with small numbers of individuals is a challenge that is likely compounded by some reliance on an oligolectic bee species for a large proportion of pollination services, although the full spectrum of floral visitors remains to be examined. In 2019, S. Schuette and C. Tracey collected a bee on *Heuchera alba* that was later identified by M. Slater as *Colletes aestivalis*, the alumroot cellophane bee, at State Game Lands 97 in Bedford County where the Raystown Branch of the Juniata River cuts through the ridge near Everett, Pennsylvania. This represented the first Pennsylvania sighting of this bee species since 1918. We have now confirmed that this bee is present throughout the Susquehanna Valley where *H. alba* populations occur, although bees were often not apparent in the smallest *H. alba* populations we encountered (all at or near the range edge). As *C. aestivalis* is a site-nesting specialist pollinator on *Heuchera* with a life cycle that mirrors the phenology of the plant, reliance on this bee has likely implications for the genetic health and reproductive capacity of *H. alba* in this region. Population genetics comparisons among and across populations (Folk et al. in prep) should provide insights related to genetic isolation of *H. alba* populations, perhaps with some insight into what we assume to be reduced capacity for gene flow among populations due to limited foraging ranges of *C. aestivalis*. A full report on the current status of *C. aestivalis* in Pennsylvania and the mid-Atlantic region is forthcoming (Sarver, in prep.).

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