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# Earl Core Student Report: How does heteroplasmy affect fitness in wild carrot?

**By Adam J. Ramsey, University of Memphis**

I receive quite a few different reactions when I tell people that I study carrot. Even better are the reactions when I clarify that I study *wild* carrot. "Wait… did you say carrot?", "What's so interesting about carrot?", or "I didn't know there was wild carrot! What's it look like?"

One interesting fact that I actually get to pass along is that wild carrot is listed as invasive in a number states in the US, many in the Southeast. In case you are wondering, I am quite sure you have seen wild carrot. The next time you are driving down the highway, look at the tall, white umbels lining the roadside. That is very likely wild carrot, or Queen Anne's Lace. Driving from Memphis to a field site in Massachusetts, I saw it virtually the entire drive. Its root is perfectly edible, given you collect it before flowering, and I hear that deep-fried umbels are delicious.

But I study carrot because individual carrots are commonly found to be heteroplasmic. Generally, we think that cytoplasmic genomes within an individual are all identical, yet they can be different from one another, and we call that mixture of genomes heteroplasmy. It is similar to nuclear heterozygosity, except that it is found in the mitochondrial or plastid genome. For instance, one of the loci my lab studies is the mitochondrial *cox1* gene. There is a SNP in the coding sequence so that there are two alleles, a 'C' and a 'T'. Some individuals have only a 'C' or a 'T', whereas others have both and are heteroplasmic.

The Earl Core award has helped to fund the first portion of my dissertation – investigating the fitness consequences of heteroplasmy. Heteroplasmy is found in humans, as it is associated with numerous diseases grouped together under the umbrella term 'mitochondrial disease'. Some cases are devastating. Yet outside of humans, very little is known about how heteroplasmy might affect fitness. Even though heteroplasmy is associated with mitochondrial diseases, there is reason to suspect that heteroplasmy does not inherently cause a decrease in fitness, particularly in plants.

First, there has been little research on non-disease associated heteroplasmy in humans. As the discovery of heteroplasmy increases over time, there is the potential that neutral or even beneficial heteroplasmic loci will be found. Second, plant and animal mitochondrial genomes largely code for the same genes, but their characteristics can differ greatly. For instance, their sizes are different (~15 kb in animals vs. 250 to 1,300 kb in plants), and recombination occurs in plant mitochondrial genomes. Of course, plants also have plastids, with similar characteristics which complicate cytonuclear interactions. The characteristics of both the plastid and mitochondrial genomes are thought to increase the likelihood of finding heteroplasmy in plants. In fact, heteroplasmy has been discovered in all sorts of plant species – rice, maize, sunflower, *Arabidopsis*, *Plantago*, tobacco, kiwi, banana, *Silene*, *Pelargonium*, alfalfa, and (yes!) carrot. Given the abundance of heteroplasmy, it seems unlikely that it is inherently detrimental. In fact, I believe that heteroplasmy, like the advantage of heterozygosity in the nuclear genome, will tend to improve fitness.

*Figure 1: The author's research greenhouse in September 2015 (left) and November 2017 (right).*

To test this hypothesis, I started a greenhouse fitness study in 2015 with 525 plants, grown from 20 accessions, five each from the Middle East, North Africa, Europe, and North America, to cover much of the range of wild carrot. I recorded germination rates and time to first leaf, and I continue to record the number of leaves at flowering, height, and number of umbels. I am also collecting pollen to determine pollen viability. Wild carrot is listed as biennial, so the projects' original timeline had the study being completed in mid-2017. In reality, carrot more accurately behaves as a monocarpic perennial. Most of my plants have lived, flowered, and died, but approximately 80 of them have yet to flower, so the project is still ongoing in its third year. Funds from the Earl Core award have helped me maintain the greenhouse and plants through this time. Once I have finished collecting the fitness data I will assay the plants for heteroplasmy at two mitochondrial loci, *apt9* and *cox1*, and one plastid indel. Using a portion of my funding, I am also going to assay 10-15 nuclear loci with PCR to account for heterozygosity which may also affect fitness. I will then be able to analyze the data to determine if heteroplasmy is associated with fitness traits.

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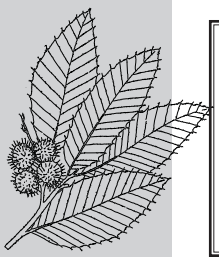

# From The Editor's Desk:

**Joe Pollard, Newsletter Editor**

I never know how many people read my ramblings in this column. If you do, you probably know I've been away for the last year on a sabbatical in the U.K. But all good things must end, so – like the Terminator – I'm back! Those who know my personal background may realize that I started going to England for graduate school way back in 1977, then married into an English family, and have made many previous visits including several extended sabbaticals. But every time I return to the United States I am struck by a subtle difference in attitudes toward exotic invasive species.

Most American botanists (and biologists more generally) have grave concerns about exotic species, and can name several noxious examples in their locale. I'm not suggesting that European scientists are unaware of the problem or fail to appreciate its urgency. But it's never completely clear what "native" means in Europe. Many of the most familiar and best loved plants in Europe may be naturalized rather than truly native, and many beautiful and iconic landscapes are anthropogenic.

Humans have been migrating across the European mainland, carrying seeds, spores, and other biological propagules with us, ever since our species left Africa. The British Isles possess some natural geographic isolation; however, travel across the English Channel has never been particularly challenging, whether for people or for the potentially invasive species that hitch-hike with us. For centuries, Britain famously had such a far-flung empire that the sun proverbially never set on it. That also meant that ships were transporting biological cargo, both intentionally and by accident. The notion of "plant protection and quarantine" (in the jargon of our own USDA) would have been an unfamiliar concept over most of this time. So the British flora includes both natives and introductions, with the latter ranging from recent arrivals to plants brought by the Romans, if not earlier visitors.

Many excellent European scientists do study all of this, using every trick in the modern toolkit including examination of historical records, pollen cores, biogeographic patterns, and genetic analysis, to name just a few. I'm not really an expert in this area, and won't go into detail on the findings. The point I'm working toward here is more about attitudes. At some level, our heightened awareness of exotic species goes along with the health and distinctness of the natural communities in our region. The Americas have only been extensively connected to global networks of trade and transportation for about 500 years. Despite many misguided introductions, we in the Southern Appalachian region are still blessed with abundant native biodiversity, and (with only a few exceptions) a clear understanding of what belongs here and what does not. Even the tragedies related to exotic invasions, like the near-extinction of American Chestnut and the current decline in Eastern Hemlock, stand in sharp relief because they are recent. If we had as long a history of biological invasions as Europe, most of us might not even realize that such species had ever been here.

So the fact that we are acutely aware of the exotic species around us may reflect the fact that we really do have spectacular native species and communities close at hand. Working to understand and protect them, and educating others to do the same, are among the most important tasks that SABS members can undertake.

## SABS Welcomes Our New Members

Larry Barden
John Butnor
Linda Fuselier
Carol Inman
Shelby Meckstroth
Alec Pierzga

***"'Hence,' Darwin advised, 'a traveler should be a botanist, for in all views plants form the chief embellishment. Group masses of naked rock, even in the wildest forms, for a time they may afford a sublime spectacle, but they will soon grow monotonous; paint them with bright & varied colors, they will become fantastic; clothe them with vegetation, they must form at least a decent, if not beautiful picture.'"***

– Mea Allan, Darwin and his Flowers. Taplinger, 1977.

# Three Remarkably Disjunct Fern Species Discovered in Pickens County, South Carolina

**By Patrick D. McMillan, Director,**
**South Carolina Botanical Garden, Clemson University**

In 2018, I identified three disjunct fern species in Pickens County: *Pellaea wrightiana* Hook., *Astrolepis sinuata* (Lag. ex Sw.) Benham & Windham ssp. *sinuata* and *Bommeria hispida* (Mett. ex Kuhn) Underw. All three species were growing on a cliff face near the Jocassee Dam. All three species are known primarily from regions far to the west of the Carolinas.

This discovery began in 2017, when Ms. Kay Wade located a large population of a strange fern growing on outcrops near the Jocassee Dam in Pickens County, South Carolina. She brought this population to the attention of local native plant enthusiast and South Carolina Native Plant Society member Mr. Dan Whitten. Dan visited the site with Kay and confirmed that the plants were a species of *Pellaea*.

Ms. Wade took me to the site on December 3, 2017 and I immediately recognized the plant as *Pellaea wrightiana* Hook., a species with which I was intimately familiar from my work in western Texas and North Carolina. I managed to scale up the rock face to secure a sample of the fronds and confirmed my identification upon my return to Clemson University.

I returned to the site with Kay Wade, Edward Pivorun and Richard Porcher on December 6, 2017 to make a more thorough examination of the cliff with binoculars. We identified two additional species: *Astrolepis sinuata* (Lag. ex Sw.) Benham & Windham ssp. *sinuata*, and *Bommeria hispida* (Mett. ex Kuhn) Underw. (This determination was suggested by Alan Weakley of the University of North Carolina after examining photographs.) We collected one frond from each of these, but the vast majority of the cliff was far outside the range of our hands and our binoculars. We returned to the site on December 13 with a member of my staff, Mr. Cody Davis, who happens to be an expert climber. Mr. Davis secured fronds of all three species.

*Figure 1. Cody Davis explores the cliff face*

The Jocassee Gorges region has long been known for the remarkable diversity of ferns found there. A review of published records and herbarium specimens, combined with field work for the preparation of this article indicates that the Pickens/Oconee county area now hosts 68 species of ferns and fern relatives. Pickens County alone is home to 65 species. The discovery of three additional species certainly places this small region into a category of extremely high regional Pteridophyte diversity.

*Pellaea wrightiana* is a common species found on acidic-reaction outcrops in Texas, Oklahoma, New Mexico, Arizona, southern Colorado and southern Utah and was formerly known from two additional populations east of Texas. The population reported here is the first record for South Carolina and, at approximately 2000 clumps, is the most extensive population in eastern North America. The closest populations to the Lake Jocassee site are in Alexander County, North Carolina (roughly 120 miles northeast) with an initially reported population of approximately 100 clumps growing on granite; and Stanly County, North Carolina (roughly 140 miles east-northeast) with an initially reported population of approximately 500 plants.

*Figure 2. Pellaea wrightiana*

*Astrolepis sinuata* ssp. *sinuata* is also a common species on acidic-reaction outcrops in Arizona and New Mexico east to central Texas. The species is remarkably disjunct from central Texas to a bridge piling in Beauregard Parish, Louisiana[1,3], and to Merriweather County, Georgia where it was found on a granite flatrock next to a natural gas distribution station (C.C. Gaddy, personal communication, 2017). The Pickens County location is the first for South Carolina, is only the second report east of the Mississippi River, and is the largest east of central Texas. The occurrence of this species in such abundance at this site indicates that it should be sought at other such locations throughout the southeastern United States.

*Figure 3. Astrolepis sinuata* ssp. *sinuata*

*Figure 4. Bommeria hispida*

The Pickens County, South Carolina location reported above represents the first known station in the eastern United States for *Bommeria hispida*. This species is impressively disjunct from the nearest known populations in Brewster County, Texas (more than 1200 miles to the southwest). This staggering distance might at first seem unique but it is identical to the disjuncture in range found in the nearby population of *Pellaea ternifolia* ssp. *arizonica*.

How did these ferns made their way from Texas or points even farther west to Lake Jocassee? The site on which all of the observations were made was a human-created habitat. The cliff habitat was created by quarrying activity for the material to build the adjacent Jocassee Dam. The entire hill and face of the mountain was denuded with no

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# Ferns *continued from p. 11*

natural vegetation left during construction. (The construction of the site can be seen on video during the opening minutes of the movie *Deliverance*.) The habitat where these ferns have colonized was barren, newly exposed rock during the construction of the dam (1968-1971).

The resulting cliff forms a horseshoe shape with the upstream portion facing south and ranging to southwest, west and northwest exposures as it proceeds downstream. The base of the cliff extends to the water for the entire length and is well over 150 feet tall along a large portion of its length. This shape in addition to the fact that the widest portion of the lake extends from the cliff habitat has created conditions that receive the full impact of the predominant southwest winds that dominate the region. The winds eddy and swirl in this cove and may provide the opportunity for enhanced settling of the spores that brought these ferns to the cliff.

It is possible that spores were transported along prevailing southwest winds and settled on the newly exposed cliff face where competition with local species was reduced or absent due to the disturbance at the site. *Astrolepis sinuata* ssp. *sinuata* (n=2n=87) relies on apogamous reproduction while *Pellaea wrightiana* (2n=116), an allotetraploid, and *Bommeria hispida* (n=30) both reproduce sexually[1,2]. Spore resiliency and longevity has been shown to be quite high in members of the family Pteridaceae with spores preserved on herbarium sheets remaining viable for over 40 years[6].

An alternative hypothesis is that nearby populations of these species resulted in colonization of the newly exposed habitat. We did a thorough search along the entire shoreline outcrop habitats of Lake Jocassee and located no other populations. We also searched the exposed rock outcrops above the cliff in vain. A look at the video mentioned earlier explains the absence of plants above the cliff as it was completely denuded during construction. It is possible that there are other populations in nearby areas that have not yet been discovered.

Another alternative hypothesis could include the introduction of spores via machinery used in the construction. Several factors would seem to argue against this proposition, notably the absence of any non-pteridophyte species from farther west on the site or nearby. Weed seeds would seem to just as easily be moved. Finally, the presence of other nearby species of ferns with a similar distribution (*Pellaea ternifolia* ssp. *arizonica*) and the presence of *Pellaea wrightiana* at two sites in North Carolina where they are assumed to have naturally colonized their habitats provide evidence that spores can travel these distances and successfully colonize new habitats.

The fact that three species, not known anywhere within hundreds or thousands of miles of the newly created habitat, managed to establish along with local xerophytic ferns is astounding. Perhaps the direction of the leading edge of the Blue Ridge Escarpment in this region of South Carolina also plays a role in the capture of spores from the southwest and points to the south and explains the presence of so many species from otherwise tropical groups in this area as well. The Blue Ridge Escarpment extends essentially in a south-southwest direction from Virginia into southwestern North Carolina. Here it turns abruptly and runs much closer to an east-west axis. The geographical orientation of the escarpment in this region is responsible for much of the climatic uniqueness of the Southern Blue Ridge Escarpment Ecoregion and in conjunction with the choices made by Duke Power in the latter part of the 20th century may have come together to provide habitat to three unique species that would otherwise never have naturally colonized South Carolina.

The result was amazing to us as ecologists, and added three species to the flora of South Carolina, one of which was the first record for eastern North America. These species may well occur other acidic-reaction rock outcrops throughout the southern Appalachian region; ecologists should continue to search for them.

All determinations were made by Patrick D. McMillan and confirmed by George Yatskievych via a loan of specimens to the University of Texas at Austin. Taxonomy follows Weakley[5]. Readers interested in further details about this discovery may consult our recent publication in Phytoneuron[4].

**Acknowledgements**

Many thanks to George Yatskievych of the University of Texas, who confirmed our identifications and patiently searched for intact sporangia to determine the subspecies of *Astrolepis sinuata* we had collected. Alan Weakley of the University of North Carolina was extremely patient and helpful in discussions concerning these ferns. I also would like to thank Brooks Wade of Jocassee Lake Tours for helping to provide the opportunity to make such discoveries possible, Zachary Maddox for providing boat transportation to the site and Rick Huffman of the South Carolina Native Plant Society for joining us and always encouraging, promoting and participating in the continued discovery of our native flora.

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***"Destroying rainforest for economic gain is like burning a Renaissance painting to cook a meal."***

– E. O. Wilson

# Edible Wild Plants:
## Beans on a Rosary: Groundnut, *Apios americana*

**by Lytton John Musselman, Old Dominion University**

In their classic treatment of edible plants of Eastern North American, the irrepressible Harvard botanist Merritt Lyndon Fernald and co-author Alfred Charles Kinsey (yes, the same Kinsey famous for his human sex research) say of the groundnut, *Apios americana*, "Probably no wild food plant of temperate eastern America so soon attracted the attention of the European colonist as the groundnut".

And rightly so. This is one of the premier edible plants in our flora—and it tastes good. Groundnut is one of the few native plants of North America that has seriously been considered for improvement as a crop. That is because all parts of the plant are edible and, being a legume, Groundnut is nutritious and is also a nitrogen fixer. (Like many "common" names, Groundnut seems a poor choice for this distinctive plant because that name is used in other countries for the peanut, *Arachis hypogea*. I think the seldom used Potato Bean is a better common name for *A. americana*).

*Figure 1. Groundnut flowers. The pinnately compound leaves are evident.*

A climbing vine that dies back to the ground each winter, Groundnut is a common wetland plant that favors the open margins of streams and lakes. It can climb up to 20 ft a season. Leaves are divided into three or five segments and are about 5 inches long. Mid-summer the attractive reddish-brown flowers appear in compact clusters (Fig. 1).

The tips with young leaves are edible and can be eaten as a steamed vegetable. By late summer the long, narrow green pods develop (Fig. 2). The young fruits can be eaten like green beans but must be collected very young to avoid the tough fibers in the fruit coat. In autumn the pods split open to release the hard, brown seeds. The mature seeds can be dried for storage. When cooked, they have the flavor of field peas (*Vigna unguiculata*). And the tubers are full of starch. In short, Groundnut is a vegetable store on a vine.

*Figure 2. Groundnut fruits.*

The tubers are nutritious and can be collected in large numbers (Fig. 3). Late fall or early winter is the best time to collect the tubers when the food is stored for the initiation of growth in the spring. Tubers should be located while the vines are still evident. They are usually located within the first foot of soil and have a distinct morphology, arranged on the stolons like beads on a rosary. For dehydration slice the tubers crosswise into discs. These store well and can be added to soups and stews.

There is one other species of the genus in our flora, *A. priceana* with the awkward "common" name of Price's Potato Bean. It is a federally endangered species that differs from the more widespread *A. americana* by —among other features — having a single, swollen turnip-like root.

*Figure 3. A cache of Groundnut tubers collected from one site in the Great Dismal Swamp in December. Tubers are produced along the stolon at regular intervals.*

# Rare Plants: Northern Starflower, *Lysimachia borealis*

**By Linda Chafin, State Botanical Garden of Georgia, University of Georgia, Athens**

I spent a lot of time this summer hiking around in north Georgia's Blue Ridge mountains (I got in some serious porch-sitting and lemonade-sipping time too). On my travels, I kept an eye out for, and sometimes even ran into, plants that are common "up north," but rare in Georgia, reaching the southern extent of their range here. This includes species such as *Lonicera canadensis, Sanguisorba canadensis*, *Sibbaldiopsis tridentata*, and *Sorbus americana*, plus another 20 or so other "northern" rarities ranked as S1, critically imperiled, by Georgia's Wildlife Resources Division.

*Lysimachia borealis (photo © Alan Cressler)*

As I visited these populations in their northern hardwood forests or rocky mountaintops, I experienced the pride I always feel that north Georgia is part of the great Appalachian mountain chain– providing habitat for genetically important peripheral populations of plants and animals.

But I also felt something new, something that I later identified as sadness. At some level, I was saying good-bye to these plants in their Georgia habitats. As yet another summer of record-breaking temperatures unfolded around me, I was forced to consider the effects

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# Botanical Brainteasers

**By Joe Pollard and Janie Marlow**

Our spring Brainteasers [Chinquapin 26(1)] were: (A) *Fagus grandifolia*, American Beech; (B) *Magnolia grandiflora*, Southern Magnolia; (C) *Platanthera grandifolia*, Large Purple Fringed Orchid; (D) *Coreopsis grandiflora*, Large-flowered Coreopsis; and (E) *Uvularia grandifolia,* Large-flowered Bellwort. (A) is the odd one out because it has the specific epithet *grandifolia* (large-leaf) whereas all the others are *grandiflora* (large-flower). Beech trees are grand in many ways, but not in their flowers, which are small and inconspicuous.

It's always good to kick off the year with a relatively straightforward contest, and this one must have fit the bill because we had 8 responses and everyone got the puzzle more or less correct. The first response we received was from first-time player Andy Warren, and he got everything 100% correct. Congratulations Andy – you're in the lead so far, but the contest goes on all year and everybody else got most of the points too. At the end of the year we'll total up the scores and decide on a winner. Playing every time is a big advantage.

Our second Brainteaser of volume 26 has a more ecological theme. As usual, provide scientific and common names for the 5 plants, and tell us which is the odd one out.

Send your answers to joe_pollard@att.net (that's an underscore character between first and last names). Email is preferred, but you can also use snail-mail to my address found elsewhere in this issue. Color photos will be posted online at http://sabs.us/publications/chinquapin-issues. Images are ©JK Marlow unless otherwise noted.






Image ©AJ Pollard

# Botanical Excursions

## Queen Anne's Lace

**Artwork by Elizabeth Ellison (www.elizabethellisongallery.com)**

*[Editor's note: In this space we would usually have an essay, or perhaps a poem, by George Ellison, accompanied by artwork by Elizabeth Ellison. On this occasion, George was tied up with other projects and couldn't write an article, but Elizabeth sent along one of her watercolors. It was a matter of sheer serendipity that the picture she sent was* Daucus carota *– wild carrot or Queen Anne's lace – the same species that Adam Ramsey describes in his Earl Core Report on the first page and below. Of course, Elizabeth's painting looks much better in color than black and white, so I urge everyone to look at the color PDF at http://sabs.us/publications/chinquapin-issues. – JP]*

Queen Anne's Lace (*Daucus carota*) while not a native to the Americas, having been introduced from Europe, is still one of our favorite flowers and is widely distributed. The leaves are edible in spring but can cause dermatitis, the roots can be eaten in spring, the flowers in summer, and the small seeds in late summer. As with all plants foraged as food, one must be certain of the identification as several highly poisonous, if not deadly, plants—Water Hemlock, for instance—look similar to it. As an artist, I love seeing Queen Anne's Lace in old pastures and along the roadside; something about the contrast in shape, color, and texture, draws my attention. And it is always there when you are driving country roads.

## Earl Core Student Report *continued from p. 9*

Funds from the Earl Core award have incidentally provided support for the third chapter of my dissertation which is devoted to understanding the effects of heteroplasmy on genome evolution. With funding from my department, I was able to sequence 48 plants from the fitness study. A pipeline has been developed that can identify each heteroplasmic SNP within the mitochondrial and plastid genomes, allowing us to ask questions about genome evolution. However, as these are fitness plants, I will also be able to more fully explore their genomes to discover which specific heteroplasmic loci are associated with fitness differences, rather than relying on three loci as in the larger study.

With the funding I have received, I have been able to continue collecting fitness data past the initial project timeline and perform PCR on the nuclear loci. I am grateful to the Southern Appalachian Botanical Society for funding this research and particularly to the awards committee for deeming this research appropriate to fund. I also thank the USDA for collecting seed from across the world which I was able to use for this study.

As luck would have it, the 2019 SABS/ASB meeting will be located in downtown Memphis, TN, a 15-minute drive from where I'm based at the University of Memphis. I'm very much looking forward to welcoming you all to Memphis and to presenting results from this research!

*Figure 2: The author with a rather large umbel of wild carrot.*

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of climate change on our high-elevation plant communities and to reckon with the likelihood of their impending loss.

As temperatures rise, our "northern species" will disappear from Georgia when they run out of higher and cooler places to retreat to. They will also be pressured from the south and from lower elevations, as vegetation from the Piedmont moves up in elevation and latitude. Somewhere on the internet I saw the Southern Appalachians described as a critical path for the northward migration of southeastern species– which is a nice thought, but it ignores the impact of the new arrivals on the existing mountain forests, which will be forever changed.

One of the rarest of the northern species in Georgia is Northern Starflower (*Lysimachia borealis*, recently transferred from *Trientalis*), a plant I've seen carpeting the floor of spruce-fir forests in Maine, but which occurs in only a handful of northern hardwood forests in Georgia. It is also ranked as critically imperiled in North Carolina, Tennessee, Kentucky, and Illinois.

Northern Starflower is a perennial herb up to 10 inches tall with a whorl of 4-8 lanceolate leaves at the top of a stem. One, two, or three white flowers open in May and are held on slender pedicels that rise from the center of the whorl of leaves, each with 5-7 pointed, petal-like lobes. The flowers fall intact, and look "like fallen stars" on the forest floor. Northern Starflower reproduces primarily by rhizomes, which spread as much as a meter from the parent plant and develop starchy tubers at their tips, each tuber bearing root and shoot buds. The parent plant and the connecting rhizomes wither and die by late fall, leaving behind several new – though genetically identical – plants in a patch. To a lesser extent, Northern Starflower also reproduces sexually. It is an obligate outcrosser, pollinated primarily by small Halictid and Andrenid bees.

As temperatures rise and rainfall becomes more unpredictable, the Southeast is expected to lose a great deal of forest to drought, wild fires, insect infestation, and wind throw. Much of our forest is predicted to transition to semi-open woodland, shrubland, or grassland. There will be a lot to mourn in the South, both ecologically and societally, as climate change proceeds. The loss of our "northern" species, and the stories they tell of rock and ice, and of ecological and genetic diversity, will be among the saddest for me.

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