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Habitat and Regeneration Requirements to Sustain Populations of *Schwalbea americana* L.

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An abstract of
A thesis submitted to the Faculty of the
James T. Laney School of Graduate Studies of Emory University
in partial fulfillment of the requirements for the degree of
Master of Science
in Environmental Sciences
2023

Abstract

Habitat and Regeneration Requirements to Sustain Populations of *Schwalbea americana* L.

By Kelly Coles

Schwalbea americana L. (Schwalbea) is a federally endangered hemiparasitic herb in the family Orobanchaceae. Habitat loss and fire suppression are the leading causes of this pyrophytic species' decline. This thesis explores propagation, soil ecology, and plant associates of the species and reports on a habitat suitability model. Chapter 1 includes an experiment in which Schwalbea was grown from seed with and without a host and with and without one of two native soil inocula collected from two sites (Parmalee and Rhexia) on Ichauway, a longleaf pine preserve in GA, USA. Seeds were more likely to germinate when inoculated with either of the inocula than when grown in sterile soil. Seedlings grown with soil inoculum from Parmalee lived longer, and lived marginally longer when grown with inoculum from Rhexia, compared to the control. Chapter 2 examines microsite characteristics using soil measurements. It examines fungal associations of Schwalbea roots. No significant differences were observed between soils in which Schwalbea was growing and surrounding soils. pH was marginally higher in soils where Schwalbea grew than those where it did not. Twenty-eight species of fungi found in Schwalbea roots were identified. Thirty-six percent of these have known beneficial effects on plants, 14% have known harmful effects, 36% have neutral-unknown effects, and 14% have mixed effects. One beneficial species identified is *Curvularia protuberata,* which forms a symbiotic relationship with a virus and the North American grass *Dicanthelium lanuginosum* (Elliott) Gould, a partnership which helps these species thrive in high temperatures. Chapter 3 reports on indicator species identified at four Schwalbea populations at Ichauway. Eleven species were found to be indicative of Schwalbea habitat at $p = 0.01$, including four graminoids, three asters, one subshrub, and three non-aster forbs. One more graminoid and non-aster forb were identified as indicators at $p = 0.05$. Chapter 4 describes the construction and evaluation of a habitat suitability model for Schwalbea. The model performed well with a test AUC of 0.924 and training AUC of 0.988. Nonmetric multidimensional scaling ordination supported future construction of a model utilizing occurrence records from localized regions rather than the southern extent of the range.

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Acknowledgments

There are many without whom I would not be where I am today. A big thank you to my advisors, Dr. Lance Gunderson, Dr. Emily Coffey, and Lisa Giencke, M.S. You all helped shape this project, asked important questions, and encouraged me every step of the way. Thank you to Dr. John Wegner for being on my committee and for sharing your treasure trove of a library and inspiring conversations with me. Thank you to the Atlanta Botanical Garden, the Jones Center at Ichauway, and Emory's Environmental Science Department for creating and funding this amazing opportunity to collaboratively study *Schwalbea americana.*

A special thank you to Lisa for teaching me the gift that never stops giving: identifying plants! Thank you for collecting soil, setting up plots, and sampling those plots from the beginning to the end with me, amongst the gnats, mosquitos, ticks, velvet ants, poison oak, and south Georgia heat! Thank you for helping me brainstorm, think problems through, and grow as a scientist. I so deeply appreciate your seemingly endless knowledge of plants and the scientific rigor (and *organization*!) you embody. Working with you has given me a strong example of the type of scientist I want to be. Thanks for, years ago, showing me a lily pond on Ichauway when I was a technician there. Thanks for unveiling the tiny distinctions that make each plant unique and for sharing delight in that chlorophyllic world.

Thank you to Allie Snyder, Jade Lee, Cami Vanderwolf, and Sara Sternick for sampling all 400 of my plots with me in the high heat of a gnatty, beautiful summer. Thank you for making me laugh, for staying positive, and for believing in me. Thank you for sharing with me what you know, from plants to music to insects to birds and beyond. I couldn't have done this without you, and you all truly filled every step of the way with joy. I am inspired by each of you.

Thank you to Joe Stockert for collecting data from my greenhouse experiment and fertilizing baby Schwalbeas while I was away doing field work through the summer and fall of 2022. Thank you to Will Hembree and John Evans for making sure the baby Schwalbeas stayed watered. Thanks to Amanda Carmichael for teaching me DNA extraction, autoclaving, and more. Thanks to Jason Ligon for teaching me about seeds.

Thank you to my sister and brother-in-law, Erin and Philip Poole, who generously made sure I had a roof over my head when I moved back to Atlanta from Asheville for this opportunity. Thanks to my niece, Mara, and dog-niece, Olivia, for making sure I got plenty of laughing and love in during the stress of the final days of writing. Thanks to the rest of my family for encouraging and supporting me: Ann and Matt Coles (Mom and Dad); Jerry and Liz Greenway (Mema and Granddaddy); Megan and Matt Johnston; Hannah and Randy Meyers; and Jason and Shawn Smith. I wouldn't be who I am and where I am today without you!

Thank you to Hazel Hendricks, who came to work one day almost ten years ago with a pair of binoculars and a plant book. You inspire me endlessly and started my plant journey's deeper dive.

Thank you to Matt Tapley, who immediately encouraged me to apply for this program even though we had just moved to Asheville. Thanks for supporting me, and for making me laugh. Thanks for making sure I took time to breathe in mountain air and sleep under the stars. Thanks for coming on Schwalbea searches with me, having a keen eye, listening to me talk about my research, and asking questions. Thanks for stopping to look at all the plants on every walk and hike. Thanks to our cat Mingo for purring cuddles and play time, which wasn't always productive but was always needed.

Lastly, I want to thank the place where most of my research occurred, Ichauway. Getting to live and work in a longleaf pine forest full of myriad, distinct habitats is an opportunity I'll always cherish. The feel of that thick air, hot, humid and ripe with the tumult of ocean even miles and miles from the sea, will forever live in my bones. Your startlingly full gusts of wind lapping sweat from my brow, your tall and sooty pines, your gopher tortoises, your canebreak rattlesnakes so still on sandy paths, your cockaded woodpeckers arcing from tree to tree, your overwhelming beauty will forever be precious to me. Ichauway was my first plunge into the incredible diversity of the North American Coastal Plain, and the plants—from common to rare—taught me so much. The afternoon storms, the dark watercolor skies, and the sound of frogs and insects fermented into medicine that fed me deep to my core. Thank you to Schwalbea for existing.

There are surely those I have neglected to thank, and though I don’t mention you in name, I hope you feel my gratitude.

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Introduction

I.1 The Longleaf Landscape

Longleaf pine (*Pinus palustris*) ecosystems spanned 36.4 million hectares (90 million acres) of the eastern United States prior to European colonization, but only about 3% of these species-rich hectares remain (Van Lear et al., 2005). Natural communities dominated by longleaf pine are incredibly variable, including upland forests, savannas, swamps, and seepage bogs in the coastal plain region and south-facing mountain ridges in Georgia and Alabama (Sorrie & Weakley, 2006). Longleaf communities are fire-dependent ecosystems with high levels of endemism comprising a large portion of the highly diverse North American Coastal Plain (NACP), which stretches from Texas east to Georgia and north along the coast to Massachusetts. Although largely ignored as a global conservation hotspot, the NACP is home to over 1800 endemic taxa of vascular plants and 56 endemic genera (Noss et al., 2015). The longleaf communities within the NACP provide habitat for 1,000 vascular plant taxa found only in these systems (Sorrie & Weakley, 2006).

Recurring fires are largely responsible for the overall biological diversity of longleaf ecosystems. Fires kill fire-sensitive oaks that could otherwise come to dominance, maintaining an open canopy of longleaf pines and a rich, sun-fed ground cover between them. Because of their thick bark, deep roots, and adaptive grass stage that protects the terminal bud of young trees from fire, longleaf are incredibly resistant to fire and in fact rely on it to thrive (Heyward, 1939).

Noss et al. (2015) and Sorrie & Weakley (2006) attribute the unique plant assemblages found in longleaf-dominated communities to more than the open habitat created by fire. The Southeastern Coastal Plain served as refuge during past glaciations and today contains microhabitats that serve as fire refugia. This land experiences sea-level fluctuations and contains extremely high soil diversity as well as subtle elevational gradients that support distinct communities in close range of each other. All these factors contribute to the importance of the Southeastern Coastal Plain in terms of plant conservation.

Many of the unique habitats of the region have been lost over the past 400 years, increasing the need for conservation. With the arrival of European colonists came mass land conversion in the unique floristic province of the longleaf-dominated Coastal Plain. Between 1600-1800, longleaf pines were overexploited for use in the naval stores industry, which required turpentine to produce the materials ships needed to sail (Frost, 1993). By 1840, longleaf had largely been removed via logging in Virginia and the industry began spreading south. As the railroad industry grew and massive logging ventures became possible, most old-growth longleaf forests were cut by the 1920's, used not just in naval stores but also in building the homes required by growing cities (Frost, 1993). While unrestrained logging was occurring, colonists' hogs were allowed to roam unpenned, and since their preferred food was the starchy longleaf seedlings, future generations were destroyed along with the diverse ground cover. Since fires were actively suppressed during this time, fire-intolerant hardwoods were able to grow at unprecedented rates, transforming the southern longleaf savannas into mixed hardwood forest (Frost, 1993).

These changes were a dramatic shift from the former sustainable management practices of the Indigenous peoples who lived with longleaf, utilizing the natural fire regimes of the region for their benefit (Frost, 1993; Van Lear et al., 2005). The suppression of fire, wild-ranging hogs, and logging ensured the demise of over 97% of the pyrophyte communities that had intimately evolved with low- to medium-intensity anthropogenic and natural fires for millennia. Although prescribed burns are once again common practice in the Coastal Plain, the possibility of natural regeneration of longleaf has been eradicated. Noss, Laroe, and Scott (1995) ranked longleaf communities as critically endangered, one of the top three most endangered ecosystems in the United States. Many species of plants and animals occurring there are threatened or endangered, including the Gopher Tortoise (*Gopherus polyphemus*) and Red-cockaded Woodpecker (*Leuconotopicus borealis*), both of whom are keystone species. These species provide burrows and cavities that are refuges from fire and homes for hundreds of species (Alavalapati et al., 2002). Hardin and White (1989) identified 191 plant taxa associated with wiregrass (*Aristida stricta* [including *A. beyrichiana*]), a key plant of longleaf pine forests, as rare or endangered somewhere across their range. One of these imperiled species is *Schwalbea americana* L.

I.2 Schwalbea americana

The monotypic perennial hemiparasite *Schwalbea americana* L. (American Chaffseed), was listed under the Endangered Species Act in 1992 with a G2 (globally imperiled) ranking (USFWS, 1992). Predominantly occurring within the historic range of longleaf, this plant occurs in the Coastal Plain south from Massachusetts to Florida (see Fig. 1). Upon listing, there were 19 known populations: 1 in New Jersey, 1 in North Carolina, 11 in South Carolina, 4 in Georgia, 1 in Florida, and 1 in Mississippi. After listing, searches were conducted for more populations, and as of the most recent five-year review in 2018, 43 extant populations are known, including several re-introduced populations and re-discovered populations in Massachusetts, Alabama, and Louisiana (USFWS, 2018). While this number is up from 1992, it has suffered oscillations as new populations have been discovered, monitored, and eventually declared lost. Seventy-two occurrences were reported in 1995. Of the populations left, only 20 are considered self-sustaining with over 100 individuals, yet the recovery goal is 50 self-sufficient populations. Primary threats to the species are habitat destruction and fire suppression.

A plant of the Gulf and Atlantic coastal plains, *S. americana* finds prime habitat in highly diverse longleaf pine savannas, sandhill-pocosin ecotones, mesic loamy-soil slopes, and fire-maintained interior woodlands (Weakley, 2020). Remaining populations occur primarily in areas subject to continued prescribed burning or frequent mowing, including quail hunting properties, forest areas managed for red-cockaded woodpeckers, a military base, powerline rights-of-way and roadsides (USFWS, 1995). The species' historic range stretched across the eastern United States south from Massachusetts to Florida and west to Texas. Inland populations were known in Kentucky and Tennessee. There is limited data available on the former prevalence of the species, but Pennell (1935) described it as "[o]ccasional or locally frequent."

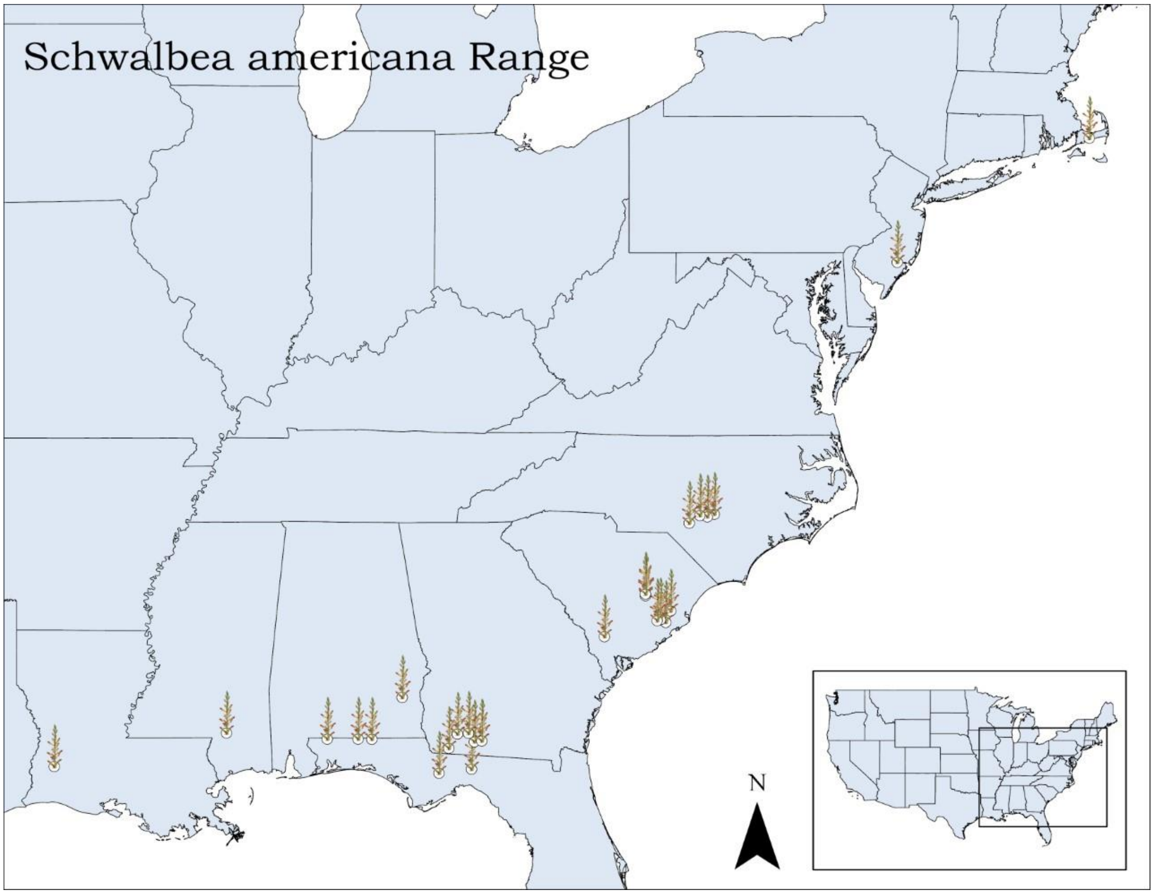


Figure 1. **Schwalbea americana *range map.*** Known distribution of Schwalbea americana in the eastern U.S. Plant icons depict approximate geographic locations, not number of populations.

First described in the scientific literature by Linnaeus in 1753, *S. americana* was named for the botanical medical writer Christian Georg Schwalbe (USFWS, 1995). The species occurs on the ancestral lands of North American Indigenous peoples, including the Muscogee and Cherokee of the Southeast, and was surely known long before being given a European name. Now considered the sole species in its genus, Pennell (1935) described both a northern and southern species: *S. americana* and *S. australis* respectively. *Schwalbea americana* was described as having mostly recurved hairs while *Schwalbea australis* was described as having upcurved hairs and wider leaves than the former, with more obscure veins. Musselman and Mann (1977) found the split of *Schwalbea* into two species to be unjustified after examining herbarium specimens, while Fernald (1937) found wide variations in leaves across the species' range, similarly supporting the contraction of the genus. Thus, this thesis will refer only to the monotypic *Schwalbea americana*, or simply Schwalbea.

Once listed as a member of the family Scrophulariaceae, molecular analysis in the late 1990's warranted restructuring of several families and Schwalbea became a member of the Orobanchaceae (Young et al., 1999). With around 1700 species and 87 genera, Orobanchaceae has a global distribution and a wide range of life history strategies from nonparasitic to obligate parasitic and includes both host-generalists and specialists (Wolfe et al., 2005). Within this family, Schwalbea is one of the basal lineages.

Figure 2. Schwalbea americana.

Schwalbea has mostly unbranched, erect stems that occasionally branch from the base, and stalkless, alternate, entire leaves, which are lanceolate or elliptic and between 2.5 and 5 cm long (USFWS, 1995; Weakley, 2020). These leaves are largest toward the base, gradually becoming narrower toward the top of the stems. All parts are pubescent, and the pedicels have two bracteoles. Green bracts subtend the bilateral tubular purplish-reddish-yellow flowers, which are 3 to 3.5 cm long, appear singly from short stalks, and are wrapped in a 5-lobed calyx. These emerge near the tops of the stems between April and June in the south, or June to July in the north, forming spike-like racemes. The plant matures into septicidal capsules between 10 and 12 mm in length that later become loculicidal. The tiny seeds inside are numerous, greenish-brown or yellowish-brown, narrow, flattened, slightly curved, and winged. They are borne inside a loose sac-like covering, which gives Schwalbea its common name (Chaffseed), and begin to mature in early summer in the south and October in the north.

A root hemiparasite, Schwalbea contains chlorophyll but also secures minerals and water from host plants through underground haustoria, which are organs that connect the xylem of host and parasite

(Těšitel et al., 2015). While they can gain many needed resources from hosts, they also must compete with them and other plants in the community for light in order to photosynthesize. To maximize nutrient gain, root hemiparasites such as Schwalbea function in ways quite different from other vascular plants. To facilitate the flow of water and nutrients from their hosts, root hemiparasites keep their stomata open day and night to create a water potential that pulls resources from host xylem into themselves (Press et al., 1988). While parasitism can of course be detrimental to the host, in many cases the effect is not substantial enough to severely harm the host and actually benefits the community as a whole (Howe, 1994; Watson, 2009). It must be noted that the family Orobanchaceae contains some severely damaging agricultural pests; however, most of the parasitic species in the family are not nearly so detrimental (Wolfe et al., 2005). Parasitic plants can in fact be incredible allies in conservation. Their parasitic habits can diminish the dominance of single species, thus increasing biodiversity. For example, the presence and survival of the parasitic *Castilleja levisecta* has been correlated with higher species richness (Dunwiddie & Martin, 2016). The litter of parasitic plants can be of a different quantity and quality than that of other species as well, further promoting subtle environmental variations where they grow (Watson, 2009).

Like many other root hemiparasites, Schwalbea is a host generalist, capable of forming haustorial connections with many different species. Still, researchers have determined preferred hosts from a range of possibilities. In the Southeast, Helton et al. (2000) found the Aster *Pityopsis graminifolia* to be the preferred host out of five species commonly occurring with Schwalbea. Although attachments occurred with all possible hosts to varying degrees, leaf area and stem length were greater with *Pityopsis graminifolia* as a host. In the northern extent of its range *Chrysopsis mariana*, another plant in the Asteraceae family, is the host of choice (Kelly, 2006).

Naturally-occurring Schwalbea populations continue to persist only in areas maintained by prescribed burning, with the exception of the New Jersey population which has mainly been managed with mowing (USFWS, 1995; Kelly 2006). Just as longleaf pine needs fire, Schwalbea too has an affinity for fire. Kirkman et al. (1998) investigated the plant’s response to fire and found that burning increased the population density of Schwalbea and its extent. This held true regardless of season of burn (winter/dormant or summer/growing). During any season tested, burning induced a flowering response and is thus capable of altering flowering phenology.

Norden & Kirkman (2004) conducted a study to better understand the factors controlling flowering responses to fire. Such responses have been attributed to a variety of factors, such as induction chemicals in smoke, heat itself, increased light availability, bursts of nutrients, release from competition, or a combination of factors (Lamont & Runcimen, 1993; McConnell & Menges, 2002; Norden & Kirkman, 2004). To tease these apart, Norden & Kirkman established four different treatments in the field examining the role of light and removal of litter: (1) fire, (2) fire and shading, (3) competing vegetation removal and stem clipping, and (4) mowing and raking. They found that a combination of above-ground stem removal and increased light availability were key to Schwalbea's flowering response, but neither was sufficient alone. These results suggest mowing as a possible management alternative on land where prescribed burning is not feasible since the mowing and raking treatment had similar flowering rates as the fire treatment. However, mowing alone would not suffice. Removing litter is also crucial for creating sufficient light conditions to induce flowering. Fuller (2016) and Norden (2002) both examined the possible role of smoke in flowering responses and propagation of Schwalbea but found no significant enhancements by utilizing smoke alone. Thus, it is known that Schwalbea requires the light and competition thinning that come with fire, but the full suite of factors necessary to elicit flowering are still unknown.

The alteration of flowering phenology in response to fire is not considered a threat to seed production given that *Schwalbea* can produce seeds in abundance even in the absence of pollinators and has a positive growth response to fire in any season (Kirkman et al., 1998; Norden & Kirkman, 2004). However, no published research has investigated the role of pollinators. Pennel (1935) assumed that bumblebees (genus *Bombus*) were pollinators based on the structure of the flowers, but there has been no published work on pollination or viability of seeds produced with and without pollinators. Additionally, Schwalbea populations are quite isolated from one another and could be experiencing genetic inbreeding as a result. Seeds predominantly produced via self-pollination could further limit genetic variability within and between populations. However, no published research has analyzed the genetics of the species or populations.

Since only 20 self-sustaining populations exist, researchers have experimented with *ex situ* propagation techniques to grow viable individuals for reintroducing and augmenting populations. In the process, many questions about Schwalbea's biology are being addressed. For instance, early research indicated that cold-stratification was not necessary for germination (Determann et al., 1997), but conservation scientists now advise cold-moist stratification for at least a month to increase germination rates (Obee & Cartica, 1997; Glitzenstein et al., 2016; Gustafson et al., 2017; USFWS, 2018).

Schwalbea can be grown without a host (Determann et al., 1997; Fuller, 2016; Glitzenstein et al., 2016; Gustafson et al., 2017). However, of the 456 seedlings grown by Glitzenstein et al. (2016), only 16.9% survived transplanting into the field, and only 75 of the total had been grown with a host. It was not reported whether there were differences in survival rates between Schwalbea grown with or without a host, but such analysis would clarify optimal *ex situ* growing conditions. In a study of preferred hosts, Obee & Cartica (1997) reported that Schwalbea grown with hosts did attain larger stature than those grown without hosts, but this was not a significant result and all the plants were less than 4 mm tall. In their study, Schwalbea seedlings were first grown alone and subsequently transplanted into containers with hosts. The significance of the timing of haustorial development is unknown, and it is possible that Schwalbea might grow better if able to connect with a host sooner after germination than this study allowed. Helton et al. (2000) placed Schwalbea seeds directly into pots containing host plants and found that plants attached to hosts had leaf areas two times greater than the unattached seedlings, and it was typically plants with larger stature that were able to survive overwintering. There were some surviving Schwalbea without haustorial connections, but those with haustorial connections had greater stem length. Those without did not attain height growth in their second growing season, even with the application of fertilizer.

Learning to cultivate Schwalbea with larger stature is an important goal for conservationists since larger plants seem to attain greater size more rapidly once outplanted and have a better chance of survival both *ex situ* and *in situ* (Kirkman et al., 1998; Helton et al., 2000; Glitzenstein et al., 2016). Although the overall survival rate was low for outplanting, Obee & Cartica (1997) found that seedlings that were transplanted last in a series of three plantings were most successful, perhaps because they had attained greater size. There is also a strong positive relationship between stem height and flowering in demographic studies of natural populations, with smaller statured individuals being both non-reproductive and at risk of higher mortality (Kirkman et al., 1998; Kelly, 2006). Thus, while it is possible to grow Schwalbea without a host, it seems likely that those grown with hosts will be more likely to survive and eventually flower in the field due to their observed gains in leaf and stem measurements.

Few studies specifically focused on reintroduction efforts exist in the peer-reviewed literature. Yet these efforts are currently taking place in New Jersey and on private lands in the southern portion of the range (personal communications with Jay Kelly & Emily Coffey). Obee & Cartica (1997) grew Schwalbea with potential hosts and then transplanted them adjacent to the natural population in New Jersey. These plants were small-statured and were provided supplemental water for 3-4 weeks and cheesecloth shade nets for a week after planting. Most seedlings perished within 18-45 days, with only 5 remaining after 70 days. Another study, in South Carolina, sought to establish a new population in suitable habitat (Glitzenstein et al., 2016). By the end of the study, just 16.9% of the outplants survived. Still, the authors pointed out measures of success. The survivors exhibited gains in growth, 6 plants reached reproductive status, and the size structure of the population was similar to a nearby natural population. Unfortunately, follow-up reports do not exist documenting the ongoing status of any reintroduced populations.

Glitzenstein et al., (2016) noted that weather seemed to influence planting success. The planting that produced the most robust individuals was correlated with high levels of precipitation, while the two plantings that failed completely occurred in conjunction with either unusually low temperatures or drought. Previous research on ground cover restoration in longleaf pine forests has indicated lack of precipitation as a key factor in failure of outplantings, so arranging irrigation in the early stages of outplanting could improve viability (Glitzenstein et al., 2001). Additionally, the plants in this study were transplanted without hosts; perhaps including hosts could achieve better outplanting results as well.

Another factor that could prove to be key for outplanting success is choosing appropriate sites. Obee & Cartica (1997) outplanted Schwalbea near an existing population, and Glitzenstein et al. (2016) chose what they described as a suitable site, but microsite characteristics might not have been considered. Kelly (2006) conducted microsite analysis for the naturally occurring New Jersey population. Using spatial analysis, he identified clustering behavior in Schwalbea. Clustering had not been recognized previously, in part due to low numbers and the ability of this species to enter prolonged states of dormancy, making spatial patterns visually unclear (Norden et al., 2004). After the New Jersey population suddenly increased fivefold between 2000-2001, Kelly (2006) plotted coordinate data from all recorded genets between 1996-2001 and found a distinct clustering pattern among them. There are distinct groups within the larger population, with uninhabited patches between. To better understand possible environmental factors influencing Schwalbea's ability to spread, Kelly collected soil from within and between colonies and germinated seeds in the different soils in a lab. While there was very high germination for the soil within the colonies, there was no germination at all in the soil between colonies. Analyzing the soils for pH, moisture, and nutrients revealed that the pH within clusters tended to be higher than between. A similar statistically significant pattern was found for soil moisture and soil carbon, which both occurred in a range in between the adjacent uplands and lowlands where Schwalbea did not grow. This data supports the idea that there are microsite requirements for Schwalbea's growth, with differences in soil even within close proximity being enough to prevent the plant's ability to germinate. This information could help explain the failure of past outplantings which chose sites based on proximity to existing Schwalbea populations alone rather than close consideration of microsite characteristics.

Kelly (2006) also analyzed indicator species as predictors of habitat suitability, which could offer a helpful tool in site selection for reintroductions in conjunction with microsite parameters. Similar studies have been conducted for other hemiparasitic plants, including *Castilleja levisecta* (Dunwiddie & Martin, 2016). In this study, many plants were outplanted and microsite characteristics and species associates were noted for survivors. The researchers found a high correlation between richness of native perennial forbs and hemiparasite survival. Research linking survivorship, indicator species presence, and microsite availability has not been conducted for Schwalbea.

One of the most pressing concerns for Schwalbea viability is the apparent lack of germination in the field (USFWS, 2018). There is no correlation between density of previous year reproductive individuals and subsequent density of seedlings, and there is no spatial correlation between previous year reproductives and next year seedlings (Kirkman et al., 1998). Despite Schwalbea seeds germinating fairly readily in laboratory conditions, *in situ* seed experiments have largely failed (Norden, 2002), and no new studies had been conducted prior to the writing of the last five-year review (USFWS, 2018). Kirkman et al. (1998) noted that there might be a correlation between microsite availability, such as pocket gopher disturbance, and seedlings. Norden (2002) tested this theory in a greenhouse and garden plot experiment and found that disturbance created by earthworm castings in the greenhouse were correlated with successful germination, but this same pattern did not occur in disturbed plots in the field. The complete lack of germination in the field was hypothesized to have been a result of drought, with no supplemental water provided to the seeds.

Another aspect of microsite that has been understudied is the soil ecology of Schwalbea. Obee & Cartica (1997), Norden (2002), and Gustafson et al. (2017) examined the effects of using different soil mixtures to propagate Schwalbea with mixed results. Obee & Cartica found no difference in vigor or survival based on soil mix while Norden (2002) found peat pellets to be the best medium. Gustafson et al. found standard nursery potting mix (50% peat: 30% perlite: 20% vermiculite) to be a satisfactory growth medium. Their experimental design combined an investigation of seed source, growth media, and native microbes and found there to be a significant three-way interaction among these, attributed to source population, one of which grew taller regardless of medium used. They found that in 3 of 4 combinations of source and medium, adding a native soil slurry improved Schwalbea’s growth.

As part of Gustafson et al.’s (2017) study, the authors examined Schwalbea roots grown with the native soil slurry under a microscope to measure the presence of mycorrhizae. Of 31 individuals assessed, only 3 had evidence of fungal connections, so the authors concluded that Schwalbea is nonmycorrhizal. In fact, it is often assumed that hemiparasites do not form mycorrhizal connections, instead relying on their hosts for nutrients. However, this assumption has not been thoroughly tested, and researchers have determined that at least some hemiparasites do indeed form both haustorial and mycorrhizal connections. Li and Guan (2008) studied 29 species of *Pedicularis,* a genus in the Orobanchaceae family, in China and discovered that most were both parasitic and mycorrhizal. Meanwhile, Koziol and Bever (2017) researched the effects of inoculating prairie plots with different native species of arbuscular mycorrhizal fungi sourced from reference prairies (including *Entrophosphora infrequens, Claroideoglomus lamellosum,* and *Claroideoglomus claroideum*) during restorations. They found that plots inoculated with some fungal species were dominated by a highly desirable diversity of late-successional forbs while non-inoculated control plots and plots inoculated with other fungi were dominated by undesirable nonnative species and weeds. Such research indicates that specific species of fungi might play unique roles in a given ecosystem. Since Gustafson et al. (2017) did not utilize a soil slurry from the individual source populations, it is possible that the fungal interactions that might occur *in situ* were not able to emerge in the greenhouse. The use of fertilizer could also have impacted the fungal-parasite relationship or lack thereof. However, their results did clearly illustrate that Schwalbea is at least capable of forming mycorrhizal connections, even if this did not occur in significant numbers. To be capable of communicating in this way, molecular mechanisms allowing plant-fungal communication must be in place, and this prerequisite is met in Schwalbea (de Freitas Pereira et al., 2018).

While determining ways to improve reintroduction and augmentation are critical goals for the conservation of Schwalbea, another way to reach the goal of 50 viable populations is to search for new populations. The most recent five-year review (USFWS, 2018) recommended searching for new populations in areas managed for quail or red-cockaded woodpeckers or areas with regular prescribed burns on 1-2 year return intervals. Key to such searches would be maps of where Schwalbea is likely to occur based on other environmental variables, such as bioclimatic variables. While no published habitat suitability model has yet been created for Schwalbea, such a model could guide future searches.

I.3 Project Overview

While much has been learned about Schwalbea since its inclusion under the Endangered Species Act, there is still more to learn if scientists are to effectively conserve the species. Details about microsite requirements, including soil ecology, and propagation techniques need further elaboration. Efforts to locate new populations of the species must also be supported to attain a goal of 50 self-sustaining populations. This thesis is one attempt to address some of these problems.

To contribute to more robust propagation techniques, Chapter One of this thesis focuses on an experimental study to determine optimized conditions for growing the species in greenhouse settings. It addresses ongoing questions concerning host and soil requirements, including: Does growing Schwalbea with a host increase its growth rate and survivability? Does the addition of native soil from the site of seed sourcing enhance growth? Finally, do Schwalbea grown with a native soil inoculum form mycorrhizal connections?

Soil ecology is explored further in Chapter Two. Soil was collected from within, between, and upslope of Schwalbea subpopulations at Ichauway and analyzed for differences in elemental, physical, and nutritional characteristics to assess possible microsite delineations. Fungal relationships are also examined by sampling the roots of Schwalbea *in situ* and sequencing fungal DNA contained therein.

Chapter Three describes an indicator species analysis conducted by collecting vegetation composition data at the four populations at the Jones Center at Ichauway in southwest Georgia. This component will contribute to knowledge of species ecology *in situ*. It will aid conservationists in the selection of suitable outplanting sites and in guiding field searches for new populations.

Chapter Four describes the construction and evaluation of a Habitat Suitability Model for *Schwalbea americana*. The model was created for a wide portion of the southeastern range of Schwalbea’s habitat, including the coastal plains of Florida, Alabama, Georgia, South Carolina, and North Carolina.

Chapter 1: *Schwalbea americana* propagation efforts

1.1 Introduction

Humans are in the midst of an anthropogenic extinction crisis known as the Sixth Mass Extinction, affecting all life on Earth (Wake & Vredenburg, 2008; Maclean & Wilson, 2011; Ceballos et al., 2017). Though plants receive less public attention than animals, they too face the primary drivers of habitat loss, invasive species, and climate change. Of the approximately 435,000 terrestrial plant species described on Earth, 36.5% are considered rare (Enquist et al., 2019). Among proposed strategies for conserving plants, *ex situ* seed banking and propagating are common (Luna, 2003; Ren et al., 2012; Kunz et al., 2014; Paris et al., 2018). A goal of many recovery plans for rare species is for a target number of self-sustaining populations with a minimum number of individuals to be protected (Schemske et al., 1994). Augmentation and reintroduction efforts support this goal.

Schwalbea americana is a federally endangered hemiparasite of the Atlantic and Gulf Coastal Plain of North America with a G2 (globally imperiled) ranking (USFWS, 1992). Schwalbea is the only species in its genus and finds prime habitat in highly diverse longleaf pine savannas, sandhill-pocosin ecotones, mesic loamy-soil slopes, and fire-maintained interior woodlands (Weakley, 2020). Remaining populations occur primarily in areas subject to continued prescribed burning or frequent mowing, including quail hunting properties, forest areas managed for Red-cockaded Woodpeckers, a military base, powerline rights-of-way and roadsides (USFWS, 1995). As of the most recent five-year review in 2018, 43 extant populations are known, including several re-introduced populations and re-discovered populations in Massachusetts, Alabama, and Louisiana (USFWS, 2018). While this number is up from 1992, it has suffered oscillations as new populations have been discovered, monitored, and eventually declared lost; 72 occurrences were reported in 1995. Of the populations left, only 20 are considered self-sustaining with over 100 individuals, yet the recovery goal is 50 self-sufficient populations.

Since only 20 self-sustaining populations exist, researchers have experimented with *ex situ* propagation techniques to grow viable individuals for reintroducing and augmenting populations. In the process, knowledge of the species' biology is being expanded upon. Early research indicated that cold-stratification was not necessary for germination (Determann et al., 1997), but conservation scientists now advise cold-moist stratification for at least a month to increase germination rates (Obee & Cartica, 1997; Glitzenstein et al., 2016; Gustafson et al., 2017; USFWS, 2018).

Although a hemiparasite, *Schwalbea* can be grown without a host (Determann et al., 1997; Fuller, 2016; Glitzenstein et al., 2016; Gustafson et al., 2017). However, of the 456 seedlings grown by Glitzenstein et al. (2016), only 16.9% survived transplanting, and only 75 of the total had been grown with a host. It was not reported whether there were differences in survival rates between *Schwalbea* grown with or without a host, but such analysis could add clarification to optimal *ex situ* growing conditions. In a study of preferred hosts, Obee & Cartica (1997) reported that *Schwalbea* grown with hosts did attain slightly larger stature than those grown without hosts, but this was not a significant result, and all the plants were less than 4 mm tall. In their study, *Schwalbea* seedlings were first grown alone and subsequently transplanted into containers with hosts. The significance of the timing of haustorial (parasitic structure) development is unknown, and it is possible that *Schwalbea* might grow better if able to connect with a host sooner after germination than this study allowed. Helton et al. (2000) placed *Schwalbea* seeds directly into pots containing host plants and found that plants attached to hosts had leaf areas two times greater than the unattached seedlings. Plants with larger stature were better able to survive overwintering. There were some surviving Schwalbea without haustorial connections, but those with haustorial connections had greater stem length. Those without did not attain height growth in their second growing season, even with the application of fertilizer.

Learning to cultivate Schwalbea with larger stature is an important goal for conservationists since larger plants seem to attain greater size more rapidly once outplanted and have a better chance of survival both *ex situ* and *in situ* (Kirkman et al., 1998; Helton et al., 2000; Glitzenstein et al., 2016). Although the overall survival rate was low for outplanting, Obee & Cartica (1997) found that seedlings that were transplanted last in a series of three plantings were most successful, perhaps because they had more time to attain greater size. There is also a strong positive relationship between stem height and flowering in demographic studies of natural populations, with smaller statured individuals being both non-reproductive and at risk of higher mortality (Kirkman et al., 1998; Kelly, 2006). Although it is possible to grow Schwalbea without a host, it is possible that those grown with hosts will be more likely to survive and eventually flower in the field due to their larger stature. This would make them better able to contribute to a self-sustaining population.

Another aspect of Schwalbea's biology needing clarification is soil ecology. Do native soil microbes help Schwalbea grow better? Do mycorrhizal connections aid Schwalbea in obtaining nutrients for optimal growth? The addition of microbes in restoration projects and plant propagation is increasingly recognized as critical for success, measured in terms such as increased tolerance of stress and better transplant survival (Myers, 1993; Koziol & Bever, 2017; Corkidi et al., 2008). Still, it is often assumed that hemiparasites do not form mycorrhizal connections, instead relying on their hosts for nutrients. However, this assumption has not been thoroughly tested, and researchers have determined that at least some hemiparasites do indeed form both haustorial and mycorrhizal connections. Li and Guan (2008) studied 29 species of *Pedicularis*, a genus in the Orobanchaceae family, in China and discovered that most were both parasitic and mycorrhizal. Meanwhile, Koziol and Bever (2017) researched the effects of inoculating prairie plots with different species of fungi during restorations and found that plots inoculated with some fungal species were dominated by a highly desirable diversity of late-successional forbs, while non-inoculated control plots and plots inoculated with other fungi were dominated by undesirable nonnative species and weeds. Such research indicates that not only might Schwalbea utilize fungi for nutrient obtainment and optimal growth, but also that not all fungi will have the same effects on growth.

Gustafson et al. (2017) examined the effects of introducing native soil microbes into Schwalbea propagation in the greenhouse. Their experimental design combined an investigation of seed source, growth media, and native microbes. They found a significant three-way interaction among these, attributed to source population, one of which grew taller regardless of medium used. They found that in 3 of 4 combinations of source and medium, adding a native soil slurry improved Schwalbea's growth. The authors examined 31 plants grown in their experiment for presence of mycorrhizae but found only 3 plants with such fungal relations. However, the soil used to create the soil slurry was not sourced from either of the sites from which the seeds were sourced. Due to high variation in fungal communities even across a span of 30 cm, it is possible that the particular microbes with which Schwalbea might interact in natural communities were simply not present (Rasmussen et al., 2018). This study was also conducted in winter months in a greenhouse without supplemental heating, and fungi exhibit seasonality, with less activity in winter (Burke, 2015). The use of fertilizer might also have impacted microbial activity (Getman-Pickering et al., 2021).

It is also conceivable that the relationship between fungi and the host plant plays an important role in regulating Schwalbea's growth, and this relationship was not examined in Gustafson et al.'s (2017) study since hosts were not utilized. Sanders et al. (1993) found that *Cuscuta pentagona*, an obligate parasitic plant, was most successful at parasitizing its host in the field when the host was mycorrhizal. They also found in the lab that inoculating the host with mycorrhizae increased the parasite's growth threefold. In another study, the root hemiparasite *Rhinanthus serotinus* was grown with the host *Trifolium pratense*, which was either inoculated with mycorrhizae or not (Salonen et al., 2001). Researchers found that the biomass of the parasite increased about 73% in the presence of a mycorrhizal host, and the number of flowers produced was greater. Perhaps the inclusion of both a host and inoculation could boost Schwalbea growth in a greenhouse. Gustafson et al.'s (2017) study might not have captured the dynamics of a hemiparasite-host-mycorrhizae relationship optimally. Still, it did exhibit that Schwalbea are at least capable of forming mycorrhizal relationships.

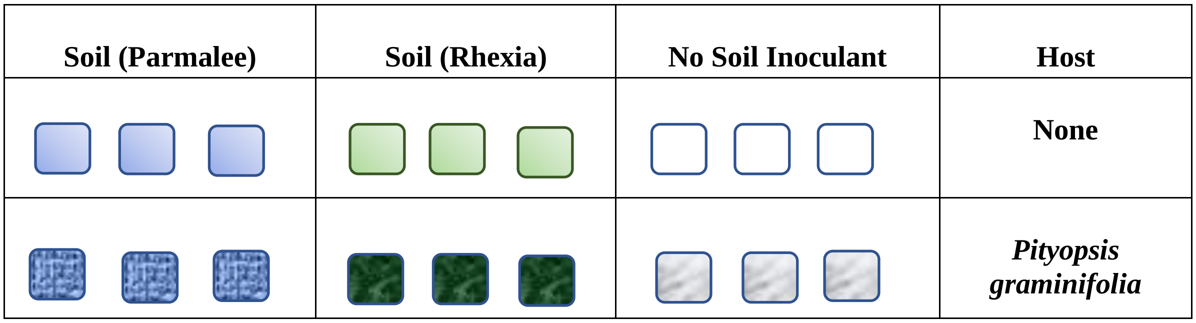
In the present study, a better understanding of Schwalbea propagation was examined to improve outplanting and augmentation success. The following questions were addressed: (1) Does growing Schwalbea with a host improve growth? (2) Does adding a native soil inoculum augment growth with or without a host? (3) Are visibly higher quality seeds more likely to germinate than visibly lower quality seeds? (4) Are there differences in germination likelihood depending on the site from which the seeds were sourced? (5) Is the length of time germinants survive dependent on host, inoculant type, seed quality, or seed source? It was anticipated that seeds grown with a host and/or with a soil inoculant would grow better in terms of height and leaf size than those grown without these factors. It was also expected that higher seed quality would positively impact probability of germination. Seeds sourced from the most vigorous site were expected to germinate more quickly and in higher proportions than other seeds. Length of survival was expected to depend on the presence of a host, an inoculant, and seed quality.

1.2 Methods

To better understand how host and native soil micro-organisms, particularly mycorrhizae, might influence the growth of *Schwalbea americana* in a greenhouse, a study was conducted at the Atlanta Botanical Garden (ABG). A 3 x 2 factorial design was used, with three replicates of approximately 15 per group (Fig. 3). Numbers were determined by available Schwalbea seed. The two factors and their levels are:

(1) Soil inoculation: soil inoculum collected from either a more or less vigorous Schwalbea site at Ichauway or no soil inoculum

(2) Host: Schwalbea grown with a preferred composite host, *Pityopsis graminifolia*, or no host



Soil (Parmalee)	**Soil (Rhexia)**	**No Soil Inoculant**	**Host**
🟦 🟦 🟦	🟩 🟩 🟩	⬜ ⬜ ⬜	**None**
▦ ▦ ▦	▦ ▦ ▦	▨ ▨ ▨	***Pityopsis graminifolia***

Figure 3. Schwalbea propagation experimental design. Soils collected from Parmalee are considered least vigorous. Soils collected from Rhexia are considered most vigorous. Each square represents a replicate of 15 pots, with 45 pots per treatment.

The Jones Center at Ichauway is a 12,000+ hectare (30,000 acre) longleaf pine reserve in Baker County in SW Georgia. It is in the Dougherty Plain, an area of karst topography, and is mostly composed of sandy soils. Ichauway supports four populations of Schwalbea which occur in ecotones between seasonally inundated wetlands and upland longleaf savannas. Soils are “transitional between poorly-drained sandy clay loams of adjacent wetlands and well-drained loamy sands or sandy loams of adjacent uplands,” (Kirkman, 1998, p. 117). The two populations from which soil was collected are Rhexia and Parmalee. Vigor was determined based on overall population trends, with one site, Parmalee, exhibiting continued loss of individuals, and the other, Rhexia, displaying population growth, with the highest numbers of individuals at Ichauway occurring in this population. These sites were chosen to examine whether soil from the more vigorous site would support healthier Schwalbea growth than the less vigorous. Soil was collected in early March 2022 using a soil corer to collect subsamples near the base of Schwalbea individuals. Subsamples were aggregated by site and sieved to remove bulky roots and rocks.

Pityopsis graminifolia (Michx.) Nutt. (silkgrass) was chosen as the host for the experiment since Helton et al. (2000) found it to be a preferred Schwalbea host and it grows readily with the natural populations at Ichauway. Silkgrass seeds collected from Ichauway in 2021 were used. Hosts were germinated in the greenhouse at ABG in January 2022. Nearly 7,000 Schwalbea seeds were collected from twelve maternal lines from populations at Ichauway in summer of 2021. A subset of 2,866 seeds from eight of the maternal lines were sorted under a microscope for likelihood of germination, with broken, moldy, or malformed seeds removed (See Fig. 4). The sorting process left a total of 754 seeds (26%) for use in the experiment. Only 230 (8% of total sorted) of these were considered best quality (Quality A). The remaining 524 (18% of total sorted) were not moldy and did not have broken embryos but either had broken chaff (papery sheath surrounding the seed itself), were smaller or thinner, or had much paler embryos and so were considered Quality B seeds. Of these 754 seeds, 189 came from Ichauway’s Rhexia site, 129 came from Pond 32, 371 came from Jericho, and 65 came from Parmalee. All seeds selected for the experiment were cold-moist stratified for a month beginning in February 2022.

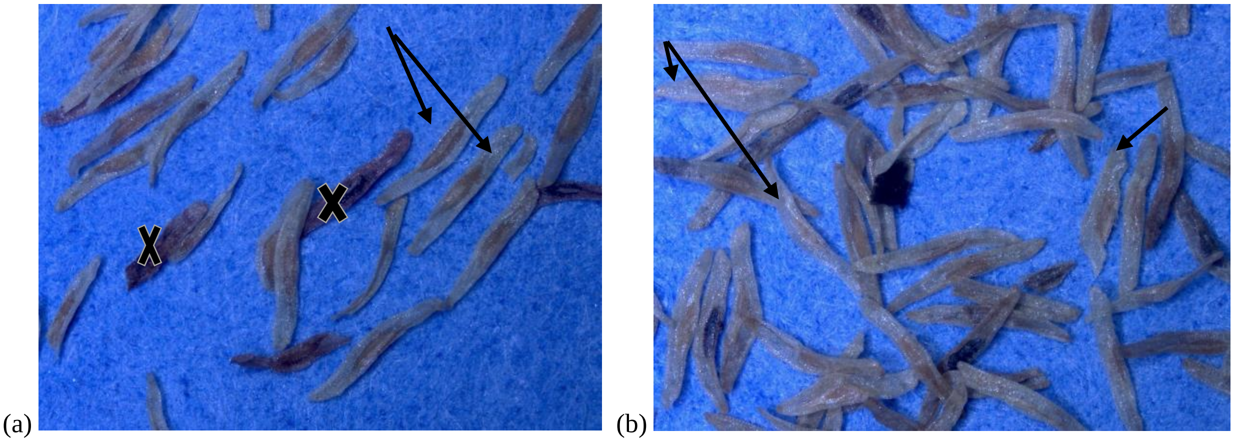


Figure 4*. *Photographs of Schwalbea seeds. (a) The arrows point to two seeds considered top quality. Note the swollen, chestnut brown, intact embryo in the center of the suitable seeds. X's mark dark, moldy seeds which were not used in the experiments. (b) The left arrows indicate empty seeds, which are almost completely translucent where the embryo should be. The bottom of these seeds is also much thinner than a top quality seed. The right arrow marks a malformed seed. Also abundant here are darkened seeds indicating mold.

Schwalbea seeding began in March 2022. Standard nursery soil (a mixture of ground pine bark and peat) was used, and it was autoclaved for 20 minutes in autoclave polypropylene bags to control for outside microbes. Two hundred and seventy 3.5-in nursery pots were used and arranged on flats with approximately 18 pots each (Table 1). All pots were filled with the same sterilized nursery soil, but pots in the inoculum treatments also received 10% inoculum by volume, from either Parmalee or Rhexia. The actual number of pots in each treatment was 90 in Parmalee, 85 in Rhexia, and 95 in the control. Approximately half the pots were in the host treatment and had a *P. graminifolia* seedling transplanted into them prior to Schwalbea seeding. To control for any possible outside microbes present on the host roots, the roots were surface-sterilized in 10% bleach solution for 5 minutes before transplanting. All pots received 2-3 Schwalbea seeds, and maternal line and seed quality were noted. Plants were watered every other day for the first month. After that, water was provided once a week and as needed. The Schwalbea seedlings were measured weekly for survival as soon as seedlings emerged in mid-April 2022. Height was to be measured once the plants matured past their first set of leaves. The original intent was to use no additional fertilizer in this experiment since fertilizer can alter the microbiome (Johnson et al., 1997). However, because of extremely slow growth rate and small-statured seedlings, the addition of fertilizer was deemed necessary. A solution of $^{3}/_{8}$ tsp of Maxsea (16:16:16 fertilizer) to 7 liters of water was used. Each pot received 2 tablespoons of solution weekly until October, when fertilizing was stopped to allow for dormancy.

Table 1. Number of seeds in experiment. Soil type and seed source names correspond with site names of different populations of Schwalbea at Ichauway. Seed Quality refers to visibly higher (A) and visibly lower (B) quality seeds.

Variable	Number Seeds	Number germinants	% germination
Soil Type			
Control	95	15	16
Parmalee	90	35	39
Rhexia	85	29	34
Host			
No host plant	150	50	33
Planted with Pityopsis graminfolia	120	29	24
Seed Quality			
A	102	21	21
B	168	58	35
Seed Source			
Jericho	107	47	15
Parmalee	35	12	18
Pond 32	63	24	18
Rhexia	65	28	15

1.3 Results

The experimental design was a 2 x 3 factorial layout to determine how seed germination and plant growth varied among two native soil types (plus a control) contrasted with the presence/absence of a host plant. The predicted outcome was that seeds grown with the most vigorous soil inoculant (Rhexia soil) and a host would outperform those grown without hosts and without an inoculant. However, due to the small number of germinants and lack of seedling growth, different data were collected.

Rather than collecting size measurements each week, only seedling germination and survival were noted. The final analysis consisted of a binomial logistic regression to determine whether the independent variables – host, inoculant type, seed source, or seed quality – influenced the binary response of germination/no germination. A seed was counted as having germinated only if it was observed for more than three weeks. This was to account for the possibility of misidentification of the seedling given that weeds also germinated in the pots and Schwalbea germinants were extremely small and difficult to identify at first. A survival analysis was conducted by building Kaplan-Meier curves based on number of weeks survived and conducting post-hoc log-rank tests to assess pairwise differences for variables with more than three levels. The more robust Cox Proportional Hazards test was conducted when the assumption of proportional hazards was met, which only occurred for the seed quality variable.

Less than 10% of the sown Schwalbea seed germinated and survived in this experiment. Out of 270 pots, only 79 ever contained germinants. Two of the 79 contained two germinants. Only 13 plants (~2% of those sown) visibly survived to October 2022, when measurements ceased and dormancy was encouraged by halting fertilizer application. All of these but two exhibited very little growth after germination, never reaching more than 2 mm in height. None were multi-stemmed. Because of limited survival and miniscule seedlings, no fungal DNA assessments were done. The original goal was to assess surviving plants for fungal DNA to determine whether the plants formed mycorrhizal connections in the greenhouse.

Twenty-eight (15% of the total) seeds from Rhexia maternal lines germinated. Rhexia germinant numbers began dropping by June 9, and no germinants were observed when measurements ceased on October 7. Twenty-four (18%) seeds from Pond 32 maternal lines germinated, but their numbers began dropping by June 3. Two remained at the end of the measurement period. Forty-seven (13%) seeds from Jericho maternal lines germinated, with numbers also dropping by June 3. Nine of these seedlings remained by October 7. Twelve seeds (18%) from Parmalee maternal lines germinated, with numbers dropping by May 20. Two seedlings remained on October 7. Of the 13 seedlings that remained, half had hosts. Ten (77%) of those remaining were growing in inoculated soils, half of which were soils from Rhexia and half from Parmalee.

A binomial logistic regression was used to assess the effects of host presence, soil inoculant type, seed quality, and seed source on germination (Table 2). Soils from both the Parmalee and Rhexia sites had a statistically significant effect on germination. Germination was 5.83 times more likely to occur with an inoculation of Parmalee soil compared to the control (z = 3.454, *p* = .001) and 4.12 times more likely to occur with an inoculation of Rhexia soil compared to the control (z = 2.607, *p* = .009). No significant effects on germination were associated with the presence or absence of a host, seed quality, or seed source.

Table 2*. *Binary logistic regression model results. Factors effecting germination. Soil type had a statistically significant effect ($p < 0.01$) on germination, with soil inocula increasing the chance a seed would germinate. None of the other factors had an effect on germination.

	Germination Model	
Variable	**Coefficient**	**z-stat**
Constant	-2.263**	-4.072
Parmalee Soil Type	1.764**	3.454
Rhexia Soil Type	1.415**	2.607
Host Presence	-0.614	-1.617
Seed Quality	0.537	1.306
Seed From Parmalee site	-0.163	-0.295
Seed From Pond 32 site	0.166	0.324
Seed From Rhexia site	0.299	0.637
AIC	202.19	
% Correct Predictions	71.26	
McFadden's-R^2	0.116	

**These coefficients are statistically significant at, at least, the .01 level.

Although seed quality was not found to effect germination, seed quality did impact the length of survival time (Fig. 5). A Cox Proportional Hazards test showed that B Quality seeds were likely to survive for longer periods in this study and were 32% less likely to experience death than Quality A seeds (z = 2.968, *p* = .003).

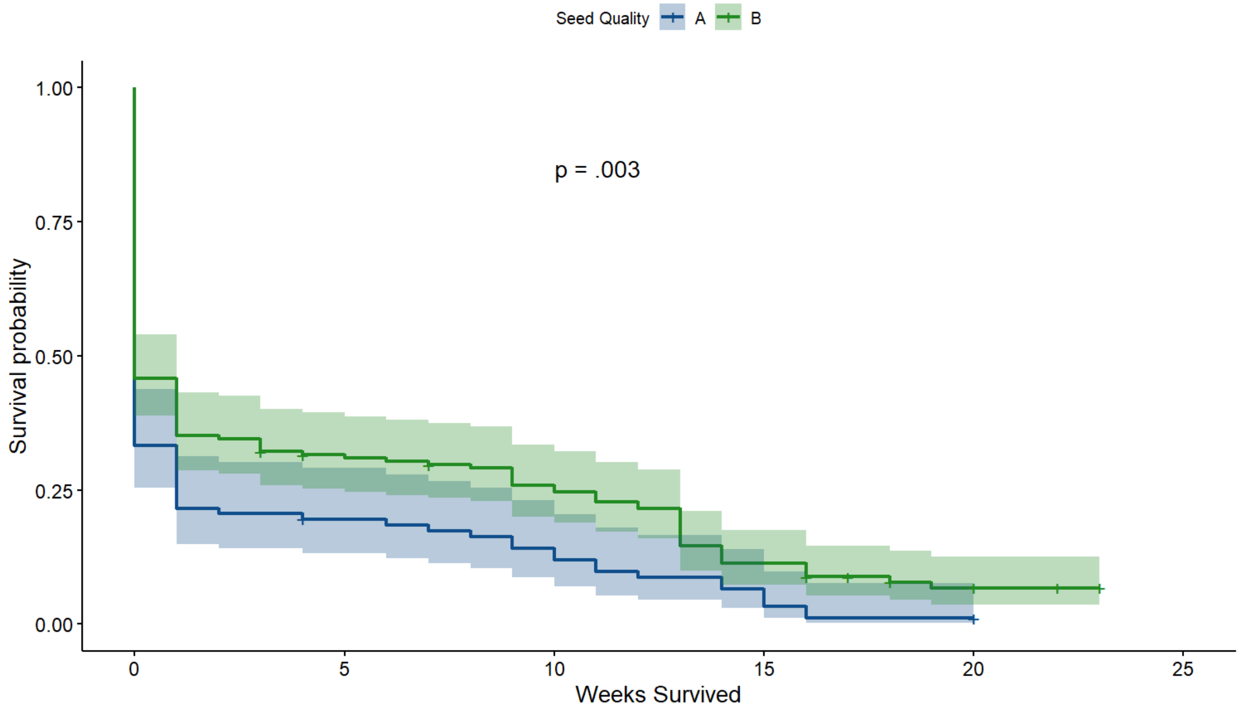


***Figure 5*. Effect of seed quality on seedling survival over time.** As shown in the Kaplan-Meier curve, seedlings from the B quality seeds outlived the A Quality seedlings over the length of the 23-week study. This difference was statistically significant.

No other variables met the proportionality assumptions of the Cox test, and thus were examined using Kaplan-Meier survival curves alone. Host presence did not affect the odds of survival (Figure 6). Seed source also had no effect on survival (Figure 7). Soil inoculant type did influence survival (Figure 8). A post-hoc log rank test showed Parmalee soil inoculation to increase the length of survival compared to the control (*p* = .035). Rhexia soil inoculation did not significantly increase survival time compared to the control (*p* = .075) or compared to Parmalee (*p* = .593). Average survival time overall was 3.67 weeks, with a range of 0 – 23.

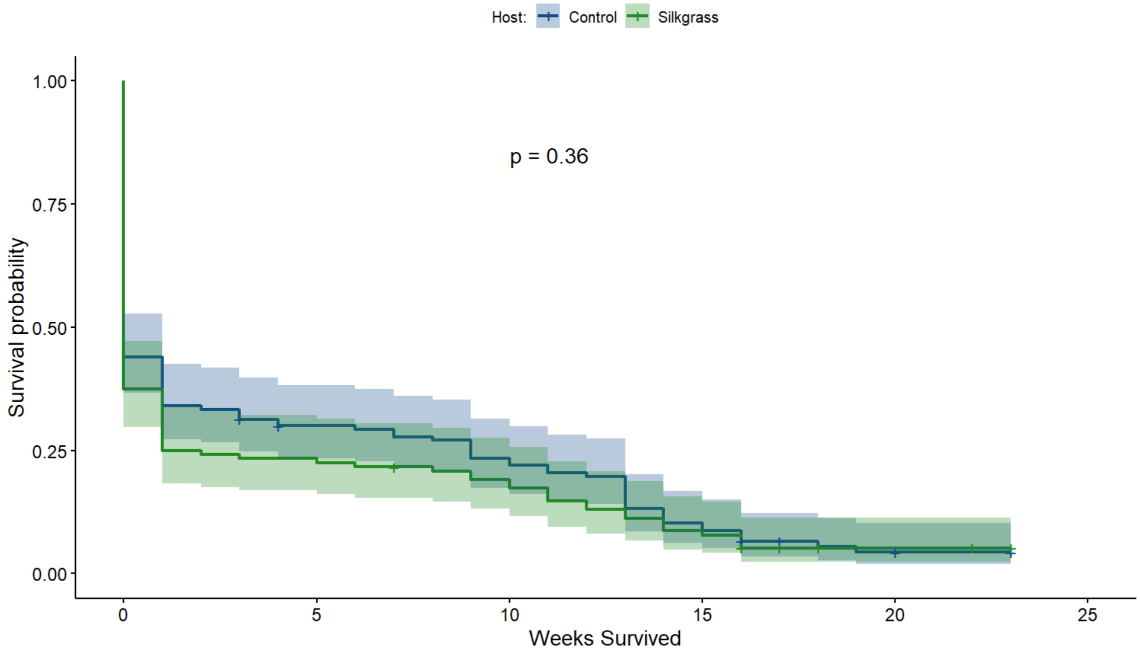


Figure 6. Effect of host plant on seedling survival over time. There was no significant difference in survival between seedlings grown with and without a host.

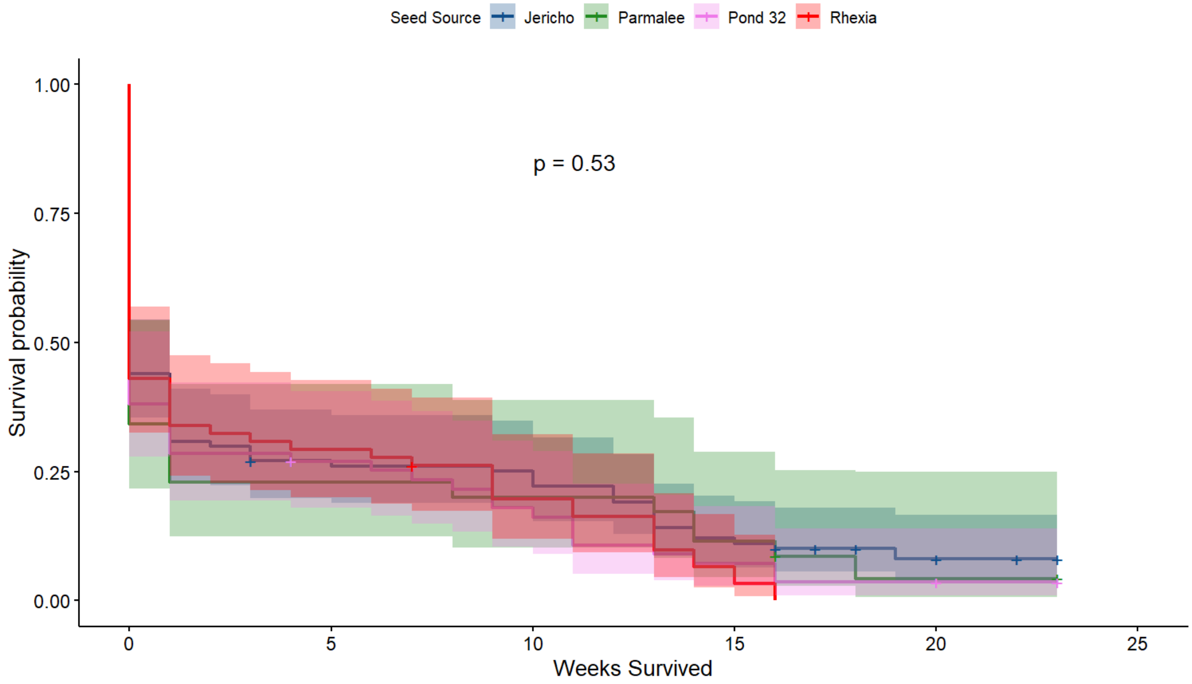


Figure 7. Effect of seed source on seedling survival over time. Seedling survival was similar among the seeds from the four study sites.

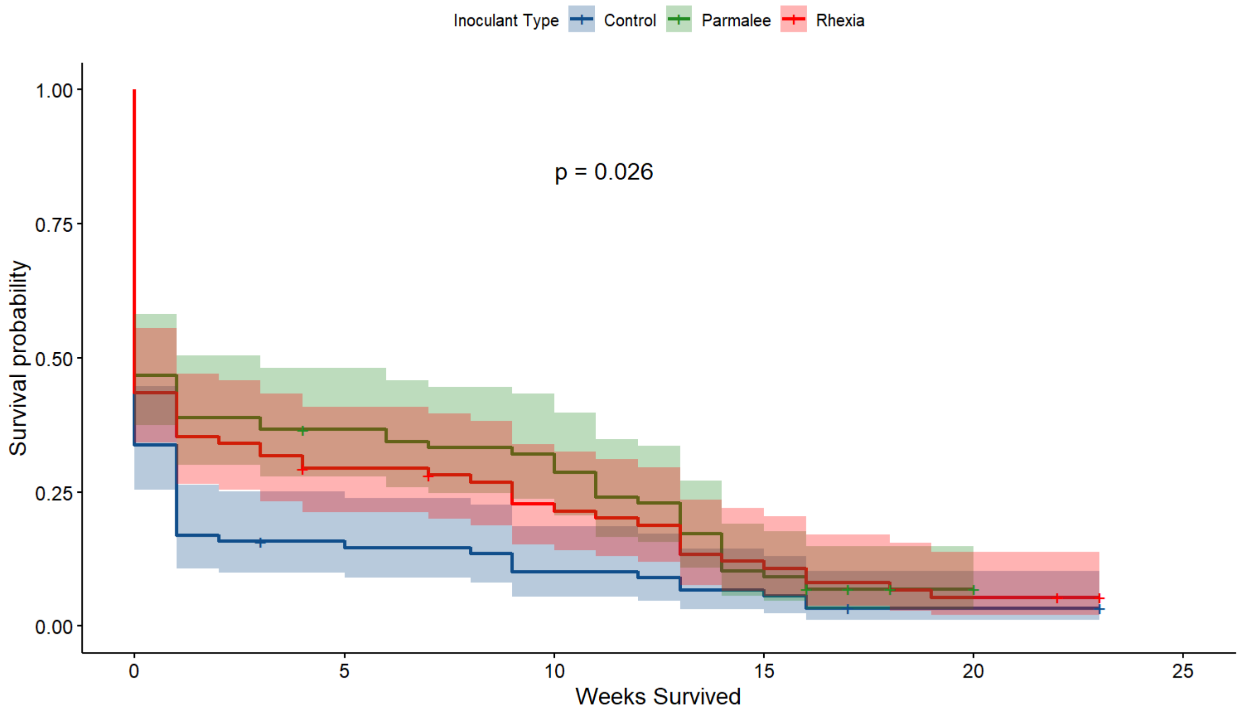


Figure 8. Effect of inoculant type on seedling survival over time. The Parmalee inoculant increased survival time significantly. The Rhexia inoculant marginally increased survival time.

1.4 DiscussionOnly about 10% of the seeds sown successfully germinated in this study. It is possible that the available seeds were not particularly viable. The process of sorting revealed large numbers of seeds to be moldy, broken, or malformed. Only 3% of the total seeds available were considered top quality, while another 8% were considered potentially viable; although, this visual classification was upended by the current study. Germination trials that took place at Ichauway prior to mailing these seeds to ABG indicated a viability rate of approximately 18% when weighted by seed count per accession and was as low as 3% for particular maternal lines.

The low germination rates observed in other germination trials and in this study could be attributed to genetic inbreeding or disrupted pollinator interactions. Although the subject has not been extensively studied, Godt & Hamrick (1998) found low genetic diversity for the species overall, within populations, and within polymorphic loci across 13 populations. Schwalbea’s disjointed populations, reliance on fire, and declining population sizes could contribute to limited genetic diversity. Additionally, the role of pollinators in seed production has not been thoroughly explored. Schwalbea can self-pollinate (Norden & Kirkman, 2004), but whether these seeds are as viable as seeds pollinated by their only observed pollinator, bumblebees, is unknown. The extent to which Schwalbea exhibits self-pollination versus cross-pollination is unknown. Pollinator populations have not been assessed at known Schwalbea sites, including at Ichauway. Potential lack of genetic diversity and the status of pollinator-Schwalbea interactions could impact the limited germination reported across Schwalbea populations *in situ* as well as in this *ex situ* study. These two factors could be important to consider in future research.

Another possible explanation for the lack of germination in this study is the choice of growing medium. Norden (2002) found peat pellets to be the best medium for Schwalbea germination, and Gustafson et al. (2016) found standard nursery (50% peat: 30% perlite: 20% vermiculite) mix to be a suitable growing substrate. Determann et al. (1997) grew Schwalbea in Nepenthes mix consisting of charcoal, sphagnum, peat, fir bark, and fern fibers. Glitzenstein et al. (2016) grew Schwalbea in both standard nursery mix (described above) and a 2:1 Jungle Growth: vermiculite mix. Since different media have been used with success, there is no standard protocol for growing this endangered plant in a greenhouse setting. In this study, a well-draining nursery mix of peat and ground pine bark was used. It is possible that the medium used in this study was simply not suitable for germinating Schwalbea.

The presence of *P. graminifolia* as a host plant had no significant effect on either survival or germination. The host plants used in this study were not well-developed. They were moderately-sized to small, and toward the beginning of the study, some were no larger than seedlings themselves. Therefore, it is unlikely that the *Pityopsis graminifolia* used in this study were truly capable of serving as hosts. Thus, this study does little to illuminate the host-parasite relationship's contributions to growth in a greenhouse setting.

Seed from the four study sites had similar rates of germination and survivorship. It was suspected that seeds sourced from the largest, most vigorous population might germinate more readily than other sources because of observed population size *in situ*. This was not the case, and seeds from all populations were equally likely to germinate. On one hand, this means that no population is inherently more viable than the others based on seed viability alone. On the other hand, none of the populations had very high seed viability rates, with an average of 23%.

Seed quality was not found to effect germination, but it was found to impact survivorship. Surprisingly, the lower quality seeds (B) were found to live longer than the higher quality (A). It was assumed that higher quality seeds would perform better than lower quality, so this finding forces the very concept of higher and lower quality seeds to change. While the lower quality seeds exhibited inferior physical characteristics as revealed by a microscope, perhaps they were actually better adapted for survival due to some unobserved attribute. Griffin (1972) and Parker et al. (2006) found that there was no correlation between seed size and percent germination. Perhaps the standards used here to assess seed quality were simply inaccurate.

It was expected that seeds grown with a soil inoculant would grow better than those without, and this was confirmed in this study. Seeds grown with either soil inoculant were more likely to germinate than those grown without an inoculant, strengthening the idea that a native microbiome is important for Schwalbea's growth. Because of low sample size, the exact likelihood probabilities reported from the logistic regression might be inaccurate. It did not seem that seeds inoculated with Parmalee or Rhexia soils germinated 5.83 times or 4.12 times more than the control. Still, the general trend holds: only 15 seeds germinated in the control, while 35 germinated in the Parmalee-inoculated soils and 29 germinated in Rhexia soils. Seedlings grown in inoculated soil were also more likely to survive for longer periods of time; however, this only applied to the Parmalee inoculation. Because the Parmalee soil was sourced from a less vigorous site, it was expected that Schwalbea grown in that inoculation would not perform as well as plants grown with the Rhexia inoculant. However, this was not the case.

It was originally thought that Schwalbea might grow better with soils from the most vigorous population due to the possibility of plant-fungal specificity. Studies have confirmed the specificity of the fungal-plant relationship in the lives of many species of orchids (McCormick et al., 2004; Shefferson et al., 2005; Jacquemyn et al., 2014). Non-orchid herbaceous plants also exhibit unique and limited patterns of fungal interactions, with the same arbuscular-mycorrhizal fungus benefitting one plant and having a neutral or negative effect on another, generating distinctive interspecific microbiomes (Adjoud et al., 1996; Wilson & Hartnett, 1998; Varela-Cervero et al., 2015; Guo et al., 2022). If a limited array of fungal species could benefit Schwalbea, then it was hypothesized that soils collected from a population with hundreds of individuals would surely be more apt to provide the appropriate microbiome for greenhouse-grown plants. However, another fungal-plant dynamic is possible.

While specialized mutualist plant-fungal relationships exist, so too do specialist pathogenic plant-fungal relations. It is possible that mutualist fungi are, in general, better able to interact with a broader assortment of plant species than antagonistic fungi are (Reinhart & Callaway, 2006; Kulmatiski et al., 2008; Cortois et al., 2016). If pathogenic fungi are dependent on particular hosts, these fungi could concentrate in soils around those hosts, a negative plant-soil feedback that has been observed to detrimentally impact plants growing in intraspecific soils (Mills & Bever, 1998; Packer & Clay, 2000; Bever, 2002; Kulmatiski et al., 2008; Petermann et al., 2008; Bever et al., 2010; Luo et al., 2019). If this dynamic were at play, it might explain why Schwalbea survived longer in soils from the less vigorous population rather than the more vigorous. Perhaps the less vigorous population had less buildup of specialized soil pathogens due to the smaller number of Schwalbea individuals.

Interestingly, Olff et al. (2000) found that soil-borne pathogens impacted the abundance of common plant species in the genera *Festuca* and *Carex*, which were self-limited by high concentrations of their own pathogens. The same study found that these species, which exhibited a response to negative plant-soil feedbacks, were able to grow on fresh soils which had been dug up by ants and rabbits and contained less pathogens. Kirkman et al. (1999) and Norden (2002) have noted that Schwalbea grows well on soils disturbed by earthworms and pocket gophers. It is possible that the relative absence of pathogenic microbes in these upturned soils (Blomqvist et al., 2000) is what allows Schwalbea to germinate in them. While negative plant-soil feedback mechanisms are increasingly understood to enhance diversity in ecosystems (Olff et al., 2000; Petermann et al., 2008; Mangan et al., 2010; Heinze et al., 2015) they could also be severely detrimental to rare and endangered plants (Klironomos, 2002). Plants such as Schwalbea already have a limited range and exhibit a low capacity to expand their boundaries. If the accumulation of pathogens in their soils *in situ* limits survivability, this could be an important avenue for future research.

Although these results point to the need for a better understanding of Schwalbea-pathogen dynamics, they also strengthen evidence that growing Schwalbea with native microbes is beneficial. The seeds in this study were more likely to germinate not just in the less vigorous Parmalee inoculum but also in the Rhexia inoculum versus the control. This indicates that although there is a possibility that pathogens are present in Schwalbea’s soils, there might also be mutualist microbes present that aid in creating conditions suitable for germination. The enhanced survivability of this plant in less vigorous soils could mean that using a site-specific inoculum is not as important as, and could even be more detrimental than, simply inoculating the growing medium with a generalized native microbiome. The long-term benefit of the Parmalee inoculum over the control for survival but not of the Rhexia inoculant over the control could be related to delayed effects of harmful microbes on the seedlings as they grow. Again, future research should focus on potentially harmful microbe-Schwalbea relationships to better understand the role such a dynamic might play in this endangered species’ decline. Studies should also explore the difference between using site-specific and generalized microbial inocula on Schwalbea survival in the greenhouse.

Chapter 2: Biotic and abiotic soil characteristics in *Schwalbea americana* populations

2.1 Introduction

Soil is critical in the development of terrestrial plant communities. Abiotic characteristics like soil texture, moisture, and mineral composition support niche differentiation among species and functional groups (Grace & Tilman, 1990; Bever et al., 1997; de Dayne et al., 2004; Raynaud & Leadley, 2004; Weil & Brady, 2017; Renne et al., 2019). Soil heterogeneity has been shown to promote diversity in grasslands and other systems and supports the coexistence of multiple plant species (Wilson, 2014; Xue et al., 2019). Although generalized responses exist in plant communities (for example, to soil fertility), individual species respond differently to such gradients, affecting composition at local scales (Daou & Shipley, 2019). Increasing homogenization across soil and other environmental variables can reduce diversity, and such homogenization is a widespread impetus for restoration (Stover & Henry, 2020). Some studies have shown heterogeneity in non-resource soil factors, such as pH and microtopography, to be especially influential in levels of species richness (Vivian-Smith, 1997; Williams & Houseman, 2013). Though abiotic components of soil are major contributors to plant niches, so too are biotic components.

A growing body of research is contributing to a deeper understanding of the ways in which soil microorganisms such as bacteria and fungi affect plant community composition (Wilson & Hartnett, 1997; Montesinos-Navarro et al., 2012; Bauer et al., 2017; Rasmussen et al., 2018). For instance, researchers are learning that some orchids exhibit specificity in their fungal associations (McCormick et al., 2004). Congenerics in the genus *Cypripedium* might grow near each other with access to the same pool of soil microbes and yet form mycorrhizal connections with different, distinct fungi (Shefferson et al., 2005). This fungal specificity encourages clustering behavior and the differentiation of niches as much as abiotic soil characteristics might (Jacquemyn et al., 2014). Rasmussen et al. (2018) found significant differences in arbuscular mycorrhizal fungi (AMF) communities between soils under heterospecific plants only 30 cm apart. While it has been assumed that all AMF are generalists, associating with a broad array of plants, the opposite is sometimes true.

Though generally appreciated, plant-fungi relationships are under-explored and could provide context to the niches of plants given how important fungi are in their growth and development. Approximately 90% of terrestrial plants rely on fungi for nutrient acquisition (Heilmann-Clausen et al., 2015). Up to 80% of plants' N and P is provided by fungi (van der Heijden et al., 2015). Researchers are discovering that there is extensive diversity in fungal communities, which exhibit varying periods of dormancy, reproductive strategies and timing, germination requirements and levels of palatability to predators (Bever et al., 2001). These factors contribute to the diversity in fungal composition on micro-scales noted by Rasmussen et al. (2018). Moreover, fungal functional differences in mutualism and parasitism affect plant species in different ways depending on species-specific relationships (Bever et al., 2001).

Fungi have important roles to play in the growth of endangered and rare plant species and could contribute to conservation efforts. Gemma et al. (2002) found that two species of endemic, endangered Hawaiian plants were more productive and vigorous when inoculated with native AMF than when grown in soils without. These plants had previously been grown without consideration of mycorrhizal requirements. Similarly, Sugiyama et al. (2019) point out that fungi are largely ignored in conservation activities but are often critical in rare plant propagation and survival. When Serna-González et al. (2019) investigated fungal associations in two endangered Magnolia species in Colombia for the first time, they found that the plant roots were heavily colonized by mycorrhizae. Since the species grow in harsh, nutrient-poor environments, it is thought that the mycorrhizae might be critical in the species' conservation.

While there are many posited reasons for the rarity of some plants, including habitat loss, Kempel et al. (2018) put forth another. Not only do plants respond to the microbiome, but they also generate them (Bever, 2003; Harrison & Bardgett, 2010; Baxendale et al., 2014; Hendriks et al., 2015). Soils conditioned by different species contain unique accumulations of pathogens and symbionts, to which plants respond differently. In Kempel et al.'s study, rare plants were more likely to respond negatively to a range of soil biota than common species. Rare plants might suffer from generalist or moderately specific pathogens more than common plants because of genetic inbreeding or because the small size of their populations limits their interactions with a diversity of pathogens and thus their acquired defenses against them. A higher susceptibility could reduce a rare species' ability to grow in new habitats, limiting their range. It could also make their own soils inhospitable by accumulating pathogens they might already possess around themselves. Thus, not only might symbiont microbes play a role in rare plant health, but predatory microbes could as well. Researchers like Johnson et al. (2012) call for a strengthened resolve to understand and document the functional importance of plant-fungal relationships. Such research could contribute much to rare plant conservation.

Schwalbea americana is a federally endangered hemiparasite of the North American Atlantic and Gulf Coastal Plain. Little is known about this species' soil ecology. However, Kelly & Denhof (2022) did find differences in soil composition between areas with Schwalbea and adjacent soils without. Analyzing the soils for pH, moisture, and mineral nutrients revealed that the pH within populations tended to be higher than in adjacent soils. Statistical differences were also found for soil carbon and moisture within Schwalbea populations compared to adjacent soils. Learning more about these distinct, localized soil gradients could help researchers better understand microsite requirements for this endangered species.

Almost nothing is known about Schwalbea's biotic soil requirements. Gustafson et al. (2017) conducted a greenhouse study in which they inoculated Schwalbea seeds with a soil slurry created from mixing native soils with water. The authors later investigated Schwalbea roots grown in this way under a microscope to measure the presence of mycorrhizae. Of 31 individuals assessed, only 3 had evidence of fungal connections, so the authors concluded that Schwalbea is nonmycorrhizal. In fact, it is often assumed that hemiparasites do not form mycorrhizal connections, instead relying on their hosts for nutrients. However, this assumption has not been thoroughly tested, and researchers have determined that at least some hemiparasites do indeed form both haustorial (parasitic) and mycorrhizal connections. Li and Guan (2008) studied 29 species of *Pedicularis,* a genus in the Orobanchaceae family, in China and discovered that most were both parasitic and mycorrhizal. Koziol and Bever (2017) researched the effects of inoculating prairie plots with different species of fungi during restorations and found that plots inoculated with some fungal species were dominated by a highly desirable diversity of late-successional forbs, while non-inoculated control plots and plots inoculated with other fungi were dominated by undesirable nonnative species and weeds. Such research indicates that not only can hemiparasites be mycorrhizal, but also that specific species of fungi interact differently with different plants. Since Gustafson et al. (2017) did not utilize a soil slurry from the individual source populations it is possible that the fungal interactions that might occur *in situ* were not able to emerge in the greenhouse. The use of fertilizer could also have impacted the fungal-parasite relationship or lack thereof. However, their results did clearly illustrate that Schwalbea is at least capable of forming mycorrhizal connections, even if this did not occur in significant numbers.

This exploratory study aims to contribute to knowledge of Schwalbea soil ecology by (1) investigating differences in abiotic soil conditions at four known populations of Schwalbea at the Jones Center at Ichauway in SW Georgia, and (2) examining whether fungi are present *in situ* in Schwalbea roots sampled from the largest of these populations. Such research will answer the questions of whether Schwalbea has abiotic site requirements, whether Schwalbea forms fungal relationships, and the nature of these relationships. It was hypothesized that microsite variability in at least the pH and carbon variables would exist and that Schwalbea would exhibit fungal connections.

2.2 Methods

Abiotic Soil Characteristics

Soil samples were collected from four populations of Schwalbea at the Joseph W. Jones Ecological Research Center at Ichauway. Ichauway is a 12,000+ hectare (almost 30,000 acres) longleaf pine reserve in Baker County in SW Georgia. It is in the Dougherty Plain, an area of karst topography, and is mostly composed of sandy soils. The Schwalbea populations here occur in ecotones between seasonally inundated wetlands and upland longleaf savannas. They are referred to here as Rhexia Subpopulations 2 & 3, Pond 32, Parmalee, and Jericho. Their soils are, respectively, well-drained Norfolk loamy sand, Orangeburg loamy sand, Duplin fine sandy loam, and Wagram loamy sand (SSURGO, 2022).

Soil samples were designated into three categories based on their location relative to existing Schwalbea individuals and subpopulations: within Schwalbea (sub)populations, between Schwalbea subpopulations, and upslope of Schwalbea (sub)populations. “Within” soil was collected within 15 cm of a Schwalbea individual. “Between” samples were collected from soils located between the delineation of Schwalbea subpopulations. Because Pond 32 is comprised of only one population, no Between sample was collected there. Finally, “Upslope” samples were collected from soils upslope of the extent of Schwalbea populations. At each site, a soil corer was used to extract approximately one pint of soil from the top 15 cm for each soil category. The corer was sanitized with ethanol between categories and between sites. Samples were thoroughly mixed according to site and category, labeled, and sent to the University of Georgia’s Soil, Plant, and Water Laboratory for analysis. The following were analyzed: pH, Texture (percent sand, silt, clay), Organic Matter (loss on ignition, LOI), Nitrate (NO3-N), Total Elements (through acid digestion), lime buffer capacity (LBC), and Total Organic Carbon.

Fungal Relationships

Seventeen root samples were collected from the most vigorous Schwalbea subpopulations at Rhexia. Five root samples were taken from Rhexia 1. The maximum possible distance between individuals there was 27 m. Six root samples were collected from both Rhexia 2 and Rhexia 3. The maximum possible distance between samples at Rhexia 2 was 14.5 m. At Rhexia 3, the maximum possible distance was 45 m. Roots were collected from vigorous individuals with multiple stems to avoid damaging individuals during sampling. It was assumed that more robust individuals would have more roots to sample from, thus minimizing overall damage. Roots totaling 0.05 grams were collected from each individual. This was accomplished by using a stainless-steel lab spatula to gently remove soil from one side of the plant’s base until a root was uncovered. The root was traced outward from the base of the plant to ensure that it was attached to Schwalbea. A lab scalpel was used to cut the root about an inch from the base. All tools were sterilized with ethanol before use between individual plants. Roots were gently scrubbed and rinsed three times in de-ionized water. They were stored in separate, labeled sealed plastic bags on ice packs in a cooler for up to two hours in the field. They were then transferred to a -80° C freezer at Ichauway.

Roots were transported on dry ice from Ichauway to the Atlanta Botanical Garden, where DNA was extracted. While not in use, they were stored in a -80° C freezer. To extract DNA, the ZymoBIOMICS DNA Miniprep Kit for microbial DNA purification was used. This kit is designed to minimize bias by thoroughly lysing all microbes. The ZymoBiomics Protocol was followed, and extracted

DNA was deposited in tubes and sent to the Zymo Research lab on dry ice for ITS sequencing. ITS refers to the nuclear ribosomal internal transcribed spacer region, which is considered the universal DNA barcode marker for fungi (Schoch et al., 2012). Large variation in the ITS region between species makes it a helpful DNA marker for use in species-level analysis.

Data analysis

Soil and fungal data were analyzed differently. To test the hypothesis that there are microsite differences between the soils in which Schwalbea grows and those upslope of or between populations, group means were compared in R. Shapiro-Wilk tests were used to test for normality of distributions. Levene tests were conducted to test for equality of variance. When variance was equal and the normality assumption was met, a one-way ANOVA test was used to compare means. If significant differences were observed, the ANOVA was followed with a post-hoc Tukey's HSD test to determine significance of pair-wise comparisons. When variance was unequal and normality was met, a Welch's one-way ANOVA was used, followed by a Games-Howell post-hoc pairwise comparison test. When normality was not met, a Kruskal-Wallis test was used to compare means, followed by a Games-Howell test if needed for pairwise comparisons. To interpret fungal ITS data, descriptive statistics were generated in R and Excel, and a literature review was conducted to learn about the species and genera identified.

2.3 Results

Abiotic soil characteristics

There were no significant differences between soils from Within, Upland, or Between Schwalbea populations (Table 3). An ANOVA failed to reject the null hypothesis that pH was the same between groups, t(2) = 3.414, *p* = 0.07. However, Upland and Within groups had marginally significant differences when comparing pairwise pH means with a Tukey's test, *p* = .059, 95% CI [-0.464, 0.008]. The Upland group has slightly higher average pH values than the Within. This relationship is explored in more detail through subsequent pH measurements of individual subplots within and outside Schwalbea populations, described in Chapter 3.

Table 3*. *Soil category means across groups. Means are for variables pertaining to (a) pH, (b) element concentrations, and (c) soil textures.

a) pH and lime buffer capacity.

Variable	**Upland**	**Between**	**Within**
LBC.eq (ppm CaCo$_3$/pH)	947	1106.5	977.2
pH	5.266	5.135	5.038

b) Element levels and plant-available nitrogen.

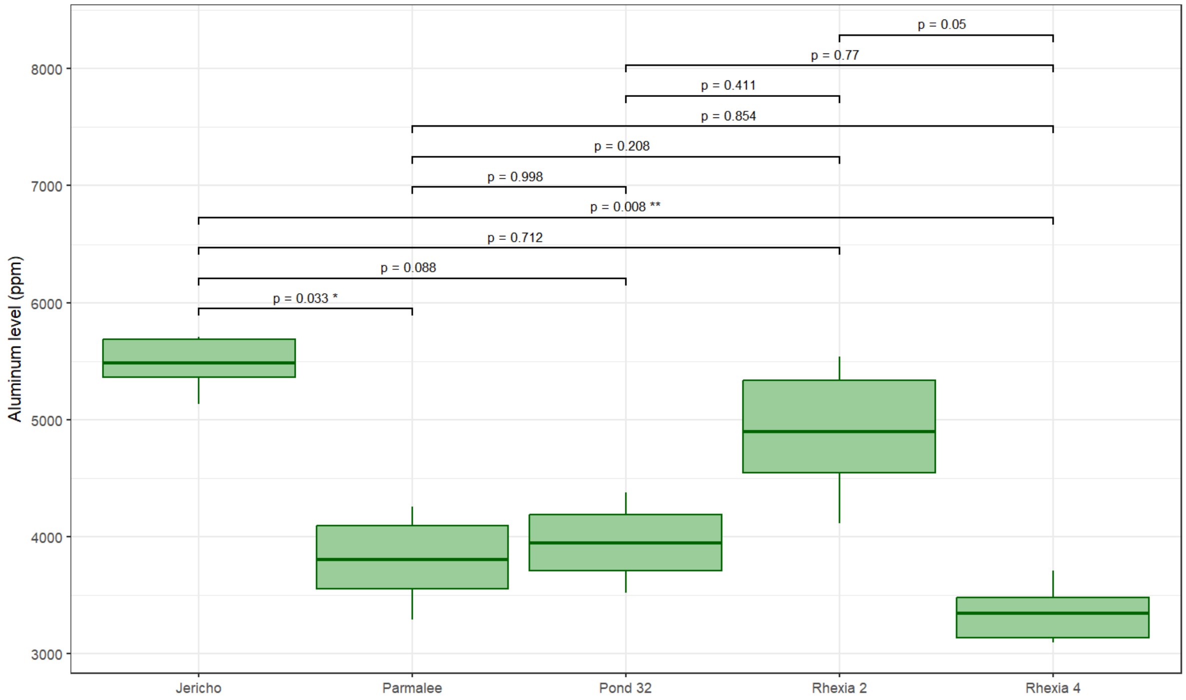
Variable	**Upland**	**Between**	**Within**
Al (ppm)	3988	4433	4562
B (ppm)	1.284	1.423	1.842
Ca (ppm)	314.2	363.75	283.8
Cr (ppm)	2.936	3.155	3.564
Cu (ppm)	2.5	2.52	2.658
Fe (ppm)	2202.4	2171.5	2424
K (ppm)	37.52	48.875	41.56
Mg (ppm)	129.8	129.55	120.58
Mn (ppm)	186.54	151.7	142.38
Na (ppm)	25	26.025	25
Ni (ppm)	1.474	1.555	2.174
P (ppm)	43.36	45.775	48.6
Pb (ppm)	4.126	4.298	5.044
S (ppm)	46.58	54.45	52.28
Zn (ppm)	2.534	2.855	4.238
NO3.N (mg/kg)	0.196	0.208	0.212

c.) Soil texture and organic carbon.

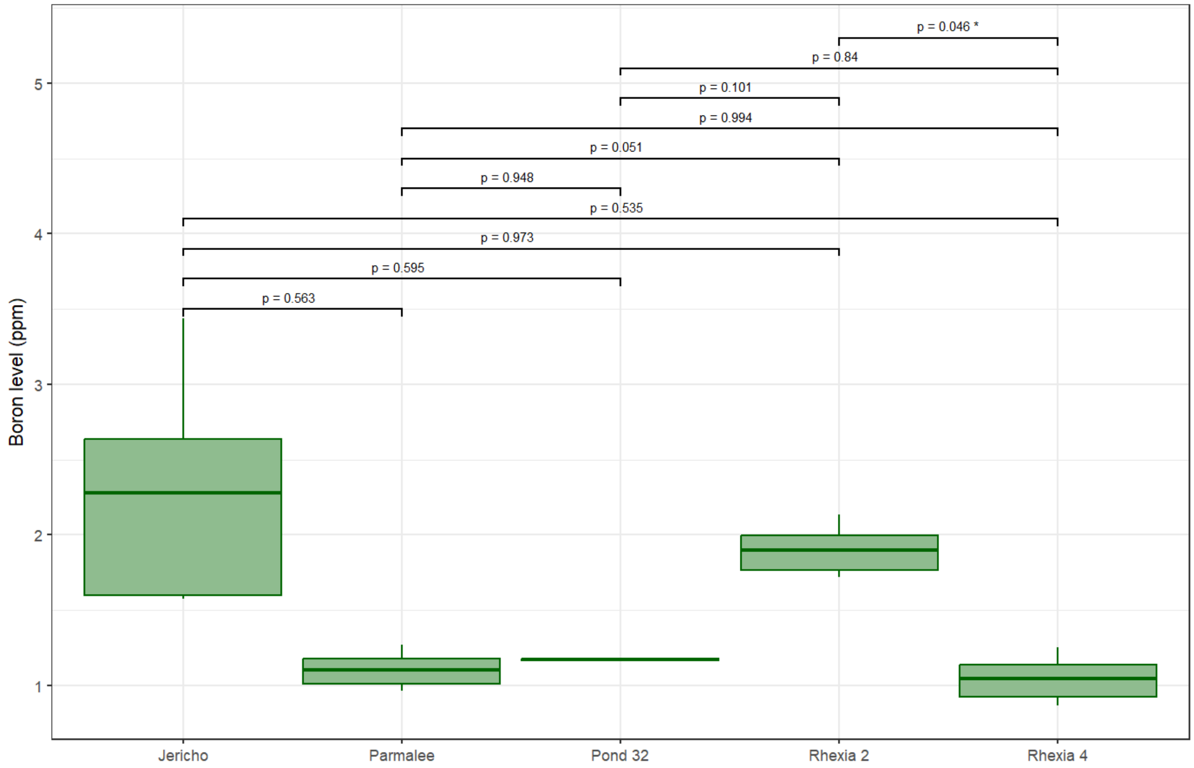
Variable	**Upland**	**Between**	**Within**
Organic Matter (%)	2.346	3.025	2.83
Sand (%)	81.86	82	80.9
Silt (%)	14.68	14.9	15
Clay (%)	3.472	3.1	4.096
TOC – Total Organic Carbon (%)	1.204	1.66	1.582

Significant differences were observed among sites for multiple soil variables (see Appendix Table A1 for site means and Table A2 for complete test results). There were significant differences in sand (F(4) = 8.326, *p* = 0.004) and silt composition (F(4) = 5.535, *p* = 0.016) between sites. Jericho had significantly lower levels of sand than Parmalee (*p* = 0.005, 95% CI [1.395, 7.005]) and Rhexia 4 (*p* = 0.007, 95% CI [1.162, 6.772]). Jericho (*p* = 0.019, 95% CI [-4.215, -0.385])) and Rhexia 2 (*p* = 0.022, 95% CI [0.318, 4.149]) both had higher silt levels than Parmalee.

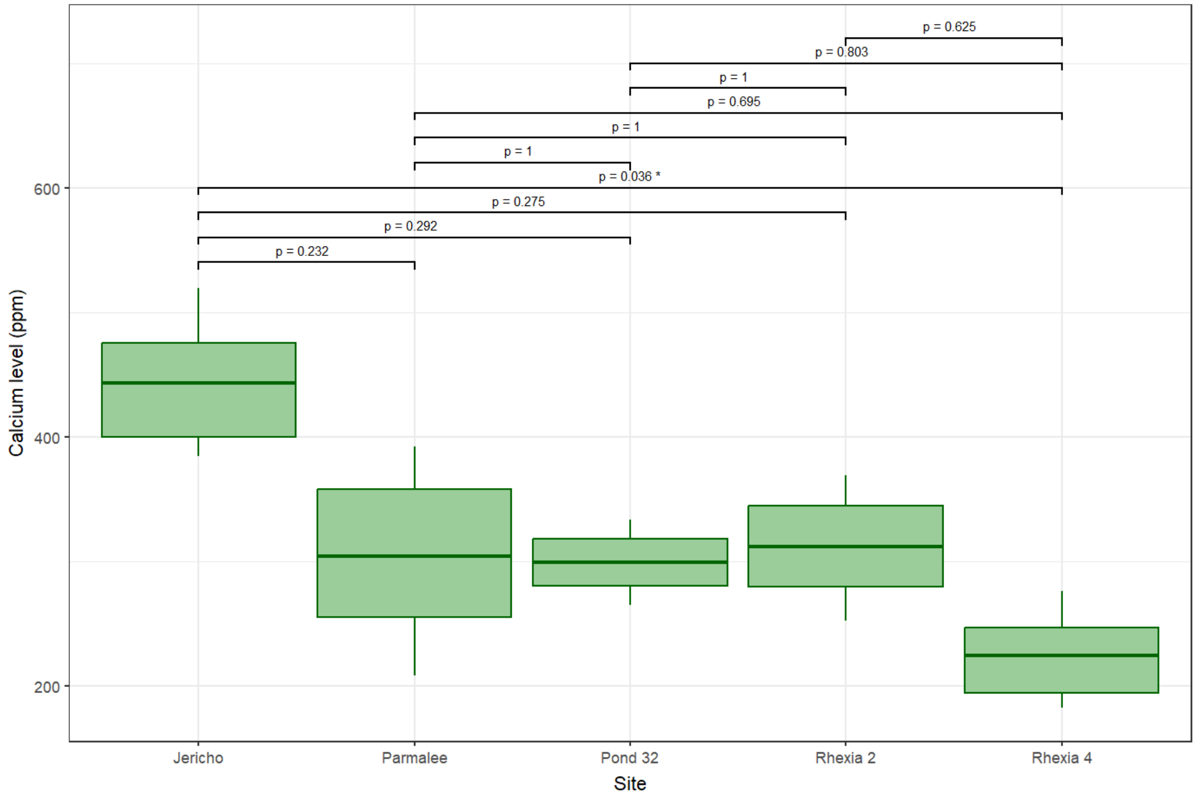
Aluminum levels at Jericho were significantly higher than levels at Parmalee and Rhexia 4 (Fig. 9a). Rhexia 2 had marginally higher Aluminum levels than Rhexia 4. Boron levels were marginally higher at Rhexia 2 than Parmalee and significantly higher at Rhexia 2 than Rhexia 4 (Fig. 9b). Calcium levels were significantly higher at Jericho than Rhexia 4 (Fig. 9c). Chromium levels were higher at Jericho than Parmalee and Rhexia 4 and marginally higher Chromium than Pond 32. Rhexia 2 had Chromium levels higher than Rhexia 4 and marginally higher than Parmalee (Fig. 9d). Iron levels were highest at Rhexia 2, which had significantly higher levels than Rhexia 4, Pond 32, and Parmalee. Jericho had significantly higher Iron levels than Rhexia 4 and marginally higher levels than Pond 32 and Parmalee (Fig. 9e). Jericho had significantly higher Magnesium levels than any site (Fig. 9f). Jericho had higher Manganese levels than Rhexia 4 (Fig. 9g). Rhexia 2 had significantly higher Sulfur levels than Parmalee, and Jericho had marginally higher levels than Parmalee (Fig. 9h). Jericho and Rhexia 2 tended to have the highest levels of these elements while Rhexia 4 typically had the lowest levels.



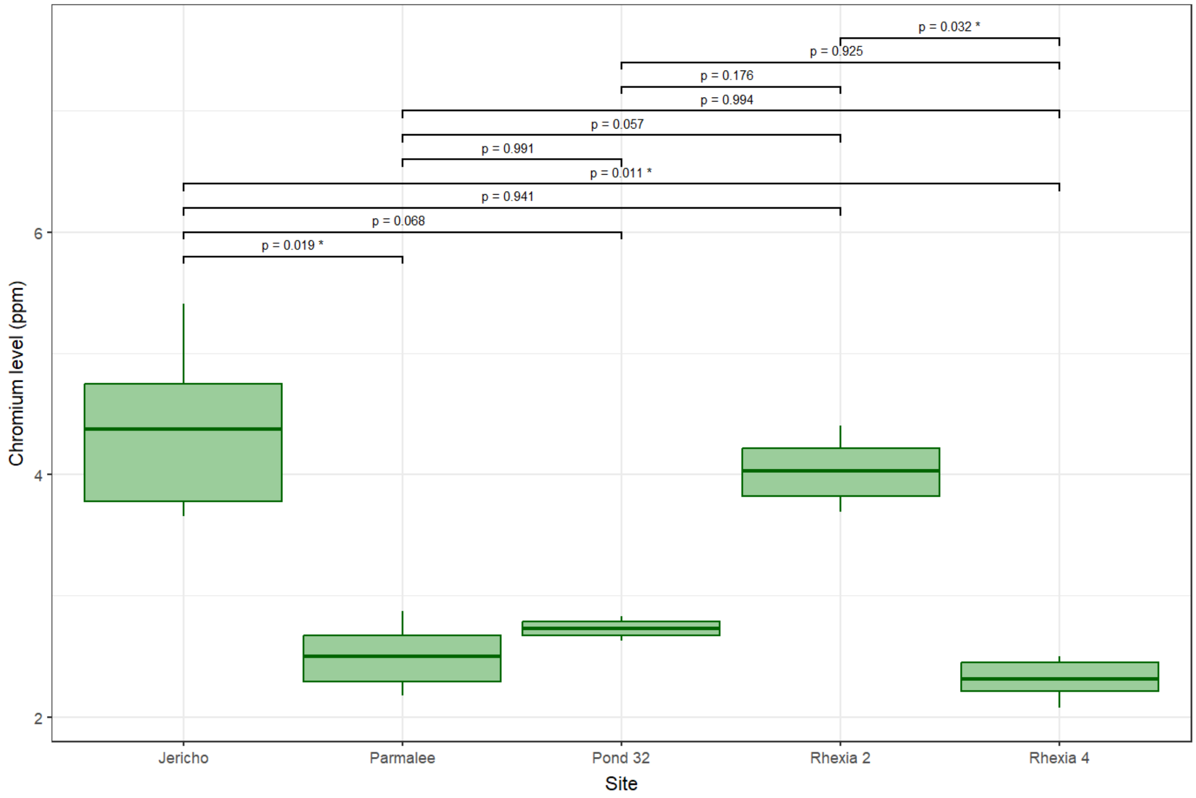
(a). Aluminum levels.



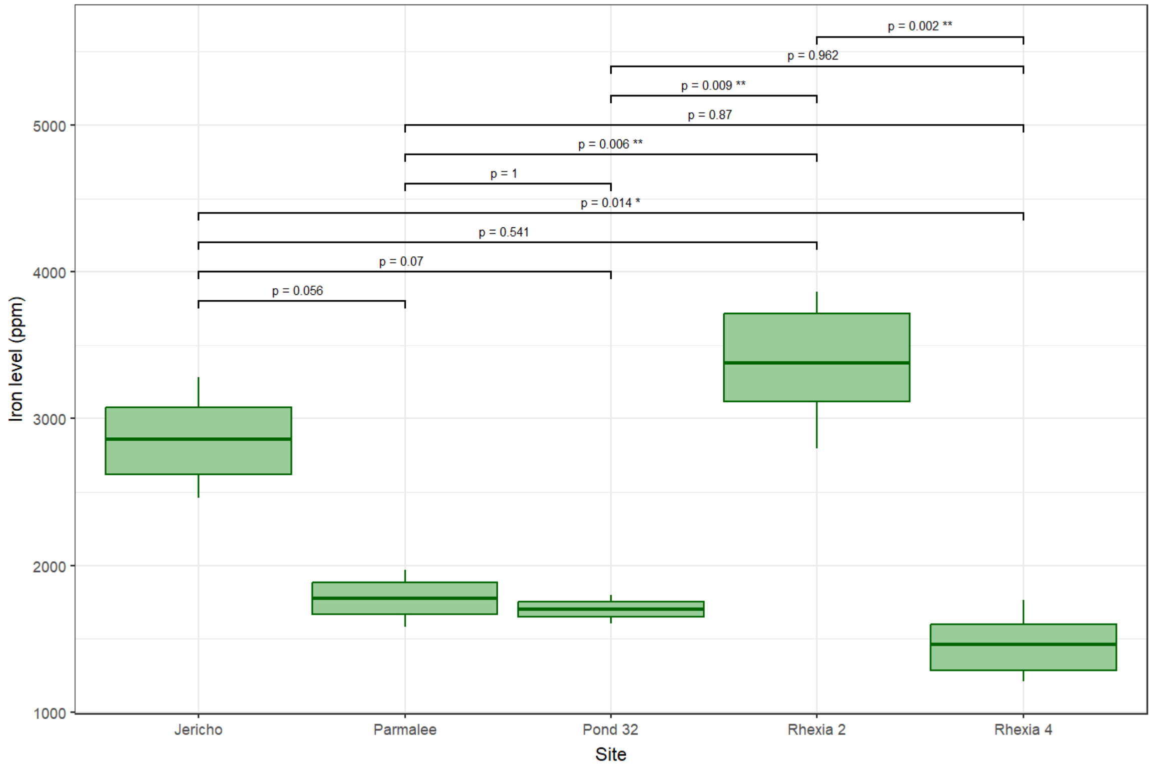
(b). Boron levels.



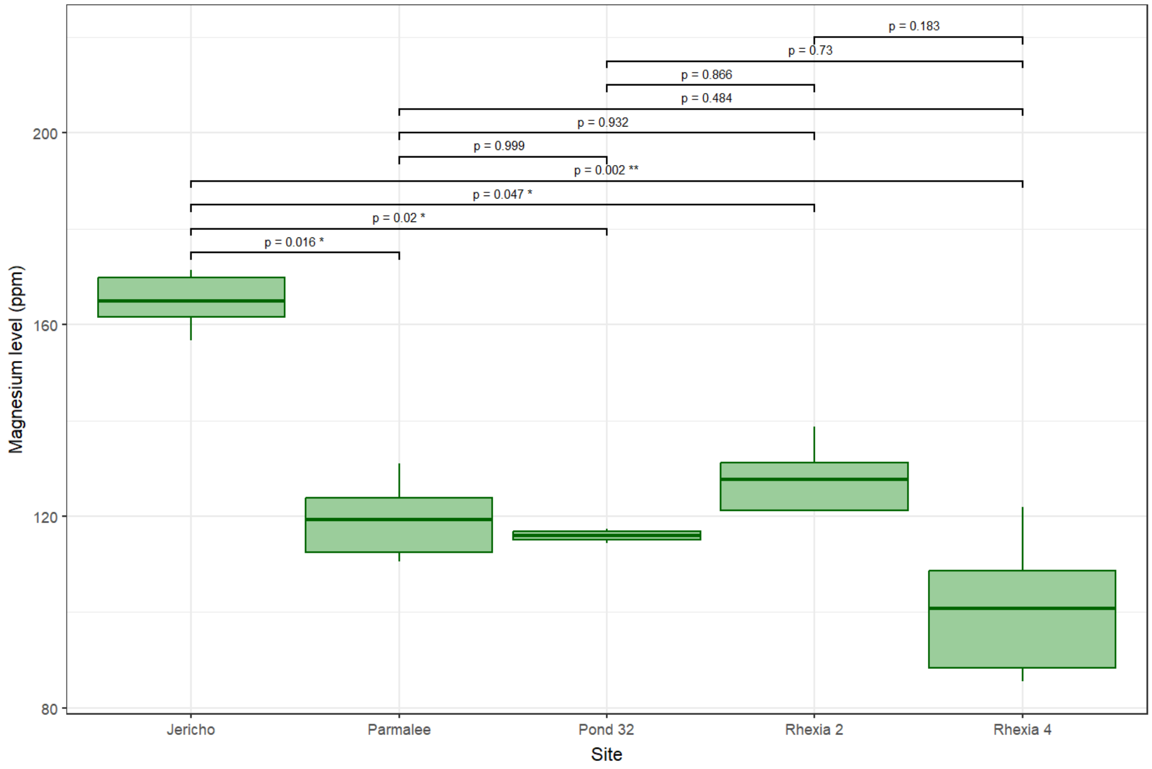
(c). Calcium levels



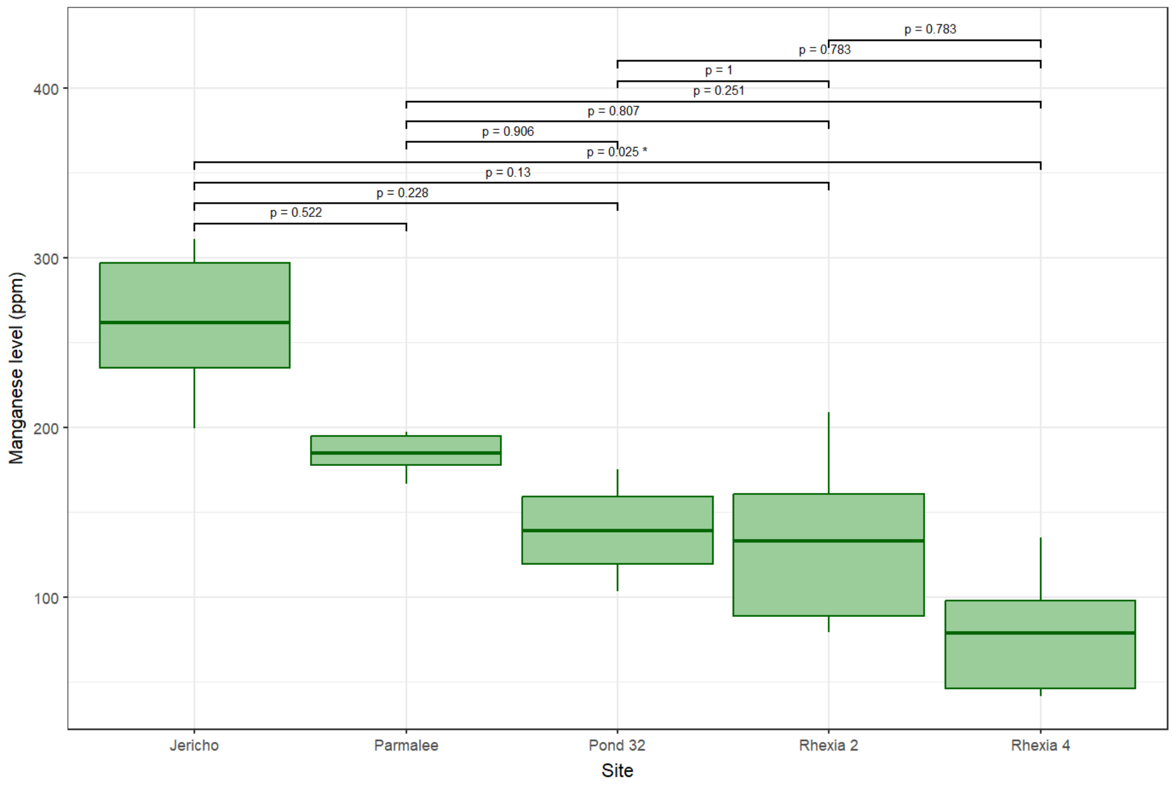
(d). Chromium levels.



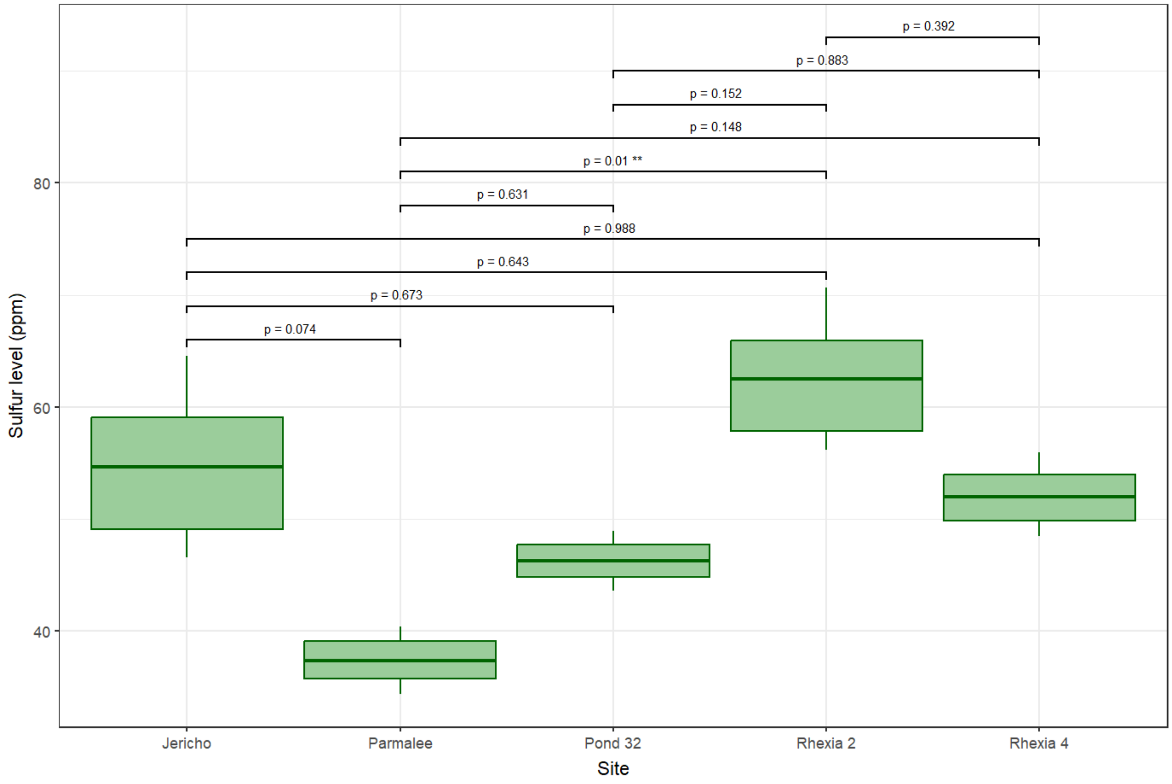
(e). Iron levels.



(f). Magnesium level.



(g). Manganese level.



(h). Sulfur levels.

Figure 9. Site mean comparisons for each element measured.

Fungal relationships

The *S. americana* roots sampled from Ichauway contained DNA from five different phyla of the Kingdom Fungi: Ascomycota, Basidiomycota, Chytridiomycota, Mucoromycota, and Rozellomycota (Fig. 10). They also contained unidentified fungi and unassigned DNA. Roots were predominantly composed of unassigned DNA, which could have been a mixture of bacterial, fungal, and Schwalbea DNA. All roots contained fungi in the Ascomycota division. Fifteen of the seventeen samples contained fungi in the Basidiomycota division. Only one sample contained DNA from the Chytridiomycota. Nine contained DNA from the Mucoromycota. Four contained Rozellomycotan DNA. There were seventeen classes, forty-one orders, seventy-one families, and seventy-three genera identified (see Appendix Table A3 for complete list). There were between 13 and 56 distinct fungal DNA sequences identified per root, with a mean of 26.94 (Fig. 11).

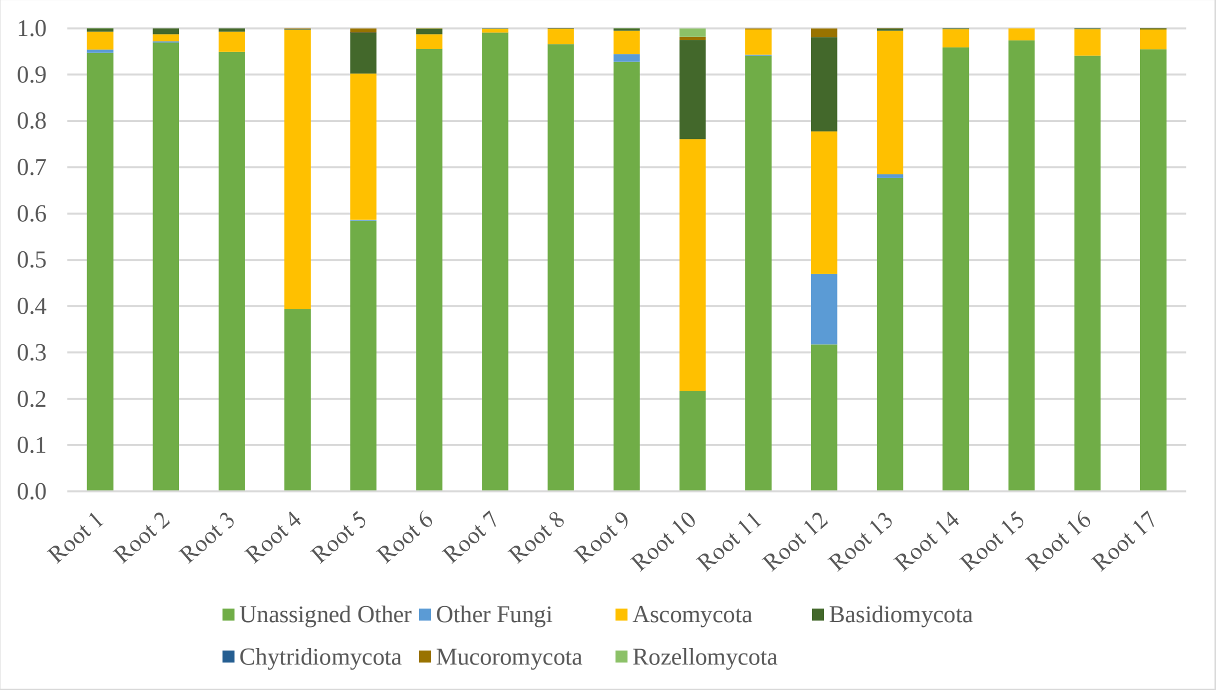


***Figure 10*. DNA composition of fungal groups found in roots of Schwalbea americana**. Numbers are percentages of five major phyla, plus unidentified "Other Fungi".

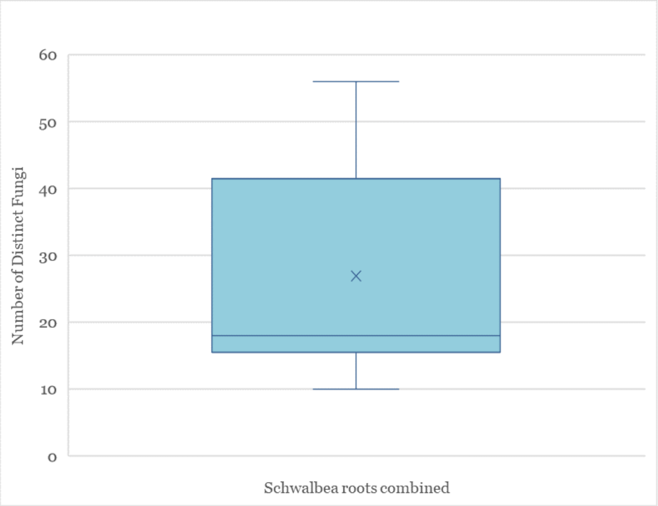
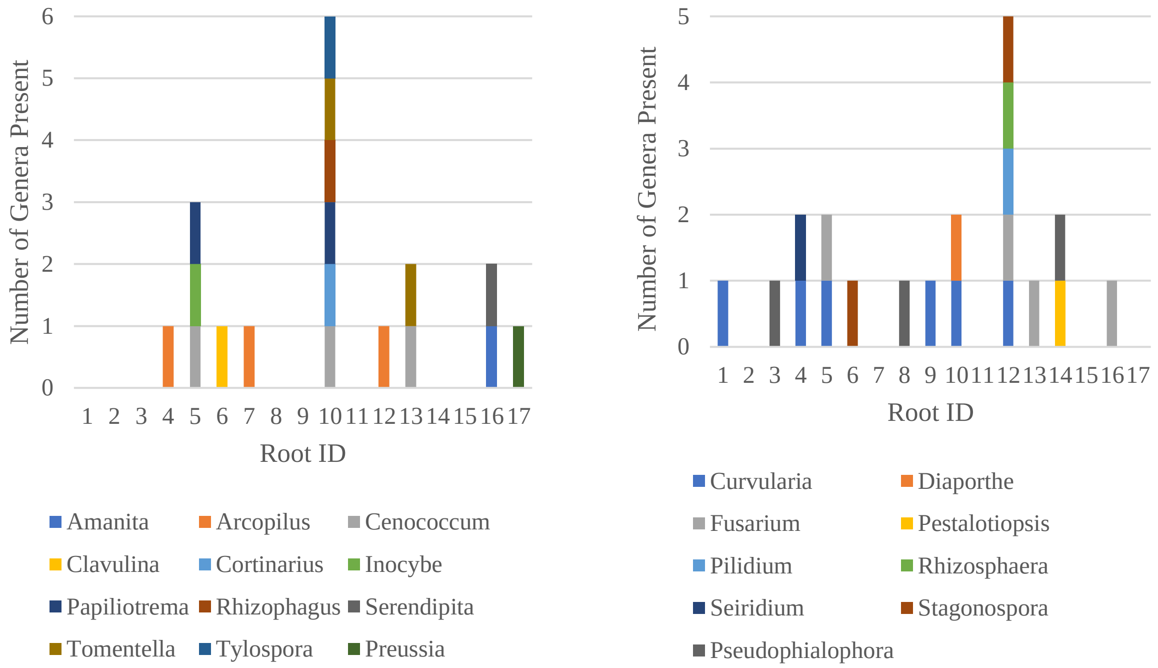


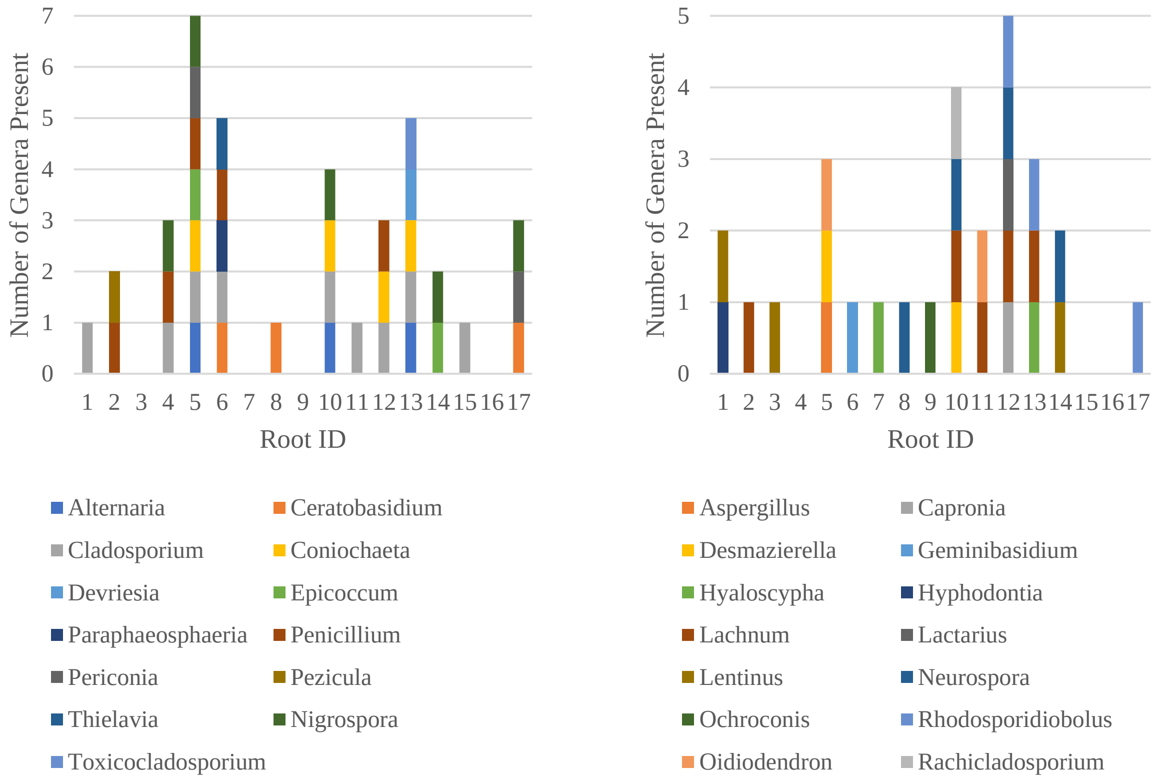
Figure 11. Fungal DNA richness found in Schwalbea roots.

The seventy-three genera identified in Schwalbea roots vary in terms of the nature of their relationships with plants. Some of these genera include known pathogenic fungi, some contain species capable of promoting plant growth, and some have neutral or unknown roles in the lives of plants. The findings from a brief literature review on the ecology of these genera are summarized in Table A4 of the Appendix. Known beneficial genera were found in just over half of the roots sampled (Fig. 12a). Known harmful genera were found in 63% of roots sampled (Fig. 12b). Genera with mixed results on plants, varying from positive to negative, were found in 68% of roots (Fig. 12c). Neutral genera were found in 74% of roots (Fig. 12d). Genera that were considered neutral but with a possibility of a positive effect on plants were also found in 74% of roots (Fig. 12e), and genera with unknown effects were found in about 58% of roots sampled (Fig. 12f).



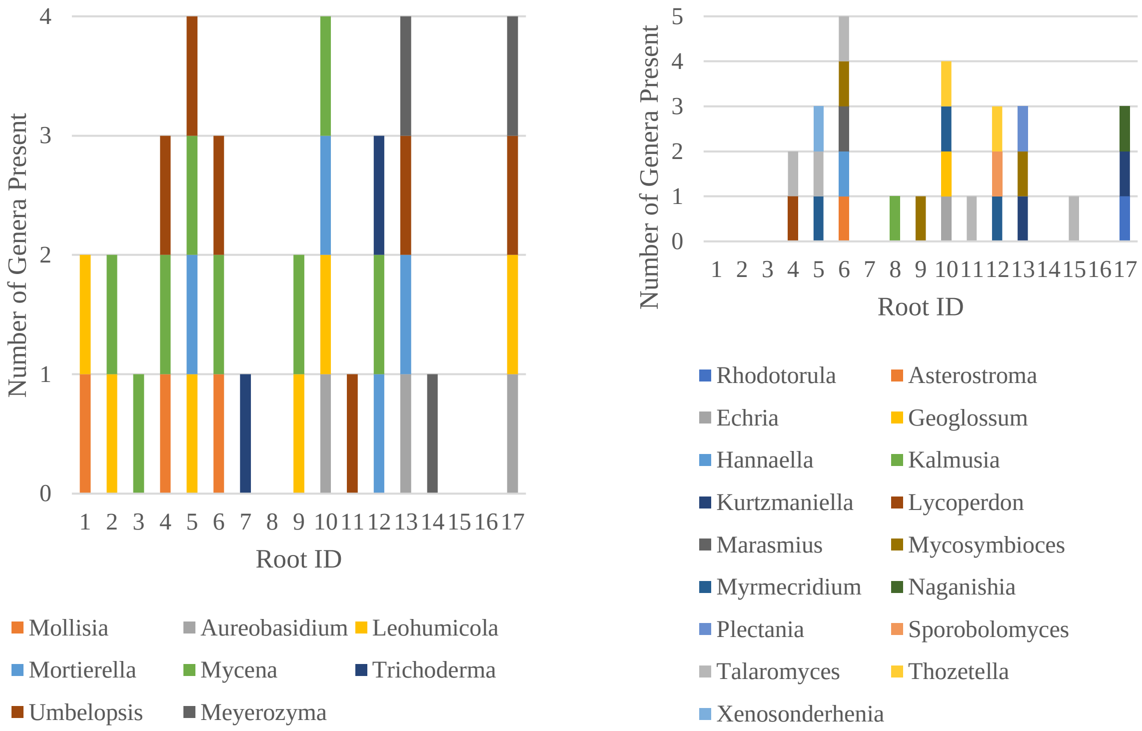
(a) Beneficial

(b) Harmful



(c) Mixed

(d) Neutral



(e) Neutral-beneficial (f) Unknown

Figure 12. Number of fungal genera in different effect-on-plant categories found in Schwalbea americana roots.

Twenty-eight sequences were identified to the species level (Table 4). Ten of the twenty-eight species are known to promote plant growth, either as endophytes or as mycorrhizal fungi. Four are known plant pathogens, causing serious disease in agricultural settings. Four have mixed effects on plants, capable of causing disease but also existing as beneficial endophytes. Ten have unknown or neutral effects on plants. Three have very little information associated with them at all. One produces edible mushrooms. One species is a known decomposer, important in the delineation of soil layers, but direct effects on plants are unknown.Two are currently being investigated for use in human industries. Three are known infectious agents in human populations, but their relationships with plants are unknown. The most frequent species was the beneficial *Curvularia protuberata*, which occurred in five (30%) roots (Fig. 13). *C. protuberata* has been found to be part of a three-way partnership with *Dicanthelium lanuginosum* (Elliott) Gould, a plant in the family Poaceae found throughout North America, and a virus (Jones, 2007). This relationship allows *D. lanuginosum* to exist in areas with high temperatures and optimizes the plant's growth. Seventeen species occurred in just one root (6% of samples). Six species occurred in two roots (12% of samples). Three occurred in three root samples (18%).

Table 4. Effect on plants of fungal species found in* Schwalbea americana *roots.

Species	Ecology	Effect on Plants
Acropilus cupreus	Capable of antifungal activity, including reducing root rot (Noireung, 2020)	Beneficial
Asterostroma cervicolor	Ectomycorrhizal and saprobic genus (Contreras-Pacheco et al., 2018)	Beneficial
Cenococcum geophilum	Ectomycorrhizal (de Freitas Pereira et al., 2018)	Beneficial
Coniochaeta hoffmannii	Known infectious agent in humans (Ellis, 2022)	Unknown
Cortinarius parvannulatus	Not much known	Unknown
Curvularia kusanoi	Known plant pathogen (Mehta et al., 2022)	Harmful
Curvularia papendorfi	Has an asexual state that causes devastating crop disease but also endophytic in some medicinal plants (Chee et al., 2015; Khiralla et al., 2020)*;*	Mixed
Curvularia protuberata	Associates with *Dicanthelium lanuginosum*, a species in family Poaceae that grows across North America, and a virus, a partnership that allows the graminoid to tolerate very warm temperatures (Jones, 2005)	Beneficial
Desmazierella acicula	A known decomposer, important in the delineation of soil layers (MicrobeWiki, 2016)	Neutral
Fusarium neocosmosporiellum	Associated with plant wilt and decline in peanuts (Obasa, 2022)	Harmful
Fusarium oxysporum	Can cause root rot and wilt, but also capable of preventing disease in its role as a root endophyte (de Lamo & Takken, 2020)	Mixed
Kalmusia italica	Capable of removing heavy metals from soils and being investigated for use in human industry (Sumathi et al., 2021)	Neutral
Lentinus squarrusolus	Produces edible mushrooms (Reena et al., 2020)	Neutral
Macrophomina phaseolina	Generalist fungus causing stem and root rot and seedling blight in at least 500 plant species around the world; capable of causing substantial loss in yield at low soil moistures and high temperatures (Marquez et al., 2021)	Harmful
Meyerozyma guilliermondii	Known infectious agent in humans (Romi et al., 2014)	Unknown
Mortierella echinula	Common species in soil, but ecological actions not described (Benny, 2009)	Unknown
Mortierella elongata	Endophyte observed to promote plant growth regardless of species; increased growth has been observed in pines, cottonwoods, oaks, grasses, tomatoes, and corn (Liao, 2021);	Beneficial
Myrmecridium schulzeri	Not much known	Unknown
Papliotrema flavescens	Can exhibit antifungal effects through competition for space and nutrition rather than creating antifungal substances; can increase resistance to wheat crown rot, (Liu et al., 2021)	Beneficial

Papliotrema terrestris	Stimulate plant growth by increasing bioavailability of some nutrients and produce chemicals that have positive effects on germination rates, (Labancová et al., 2022)	Beneficial
Periconia byssoides	Most are widely distributed saprobes and endophytes, but some are economically important pathogenic fungi on plants (Markovskaja & Kačergius, 2014)	Mixed
Rhizophagis irregularis	Arbuscular mycorrhizal fungus that aids in regulating production of primary metabolites in plants and can increase resilient plant responses to abiotic and biotic stress (Cartabia et al., 2021)	Beneficial
Rhizosphaera kalkhoffii	Fungal blight on spruce and fir planted outside their ranges, but not much else described (Ash Kanner, 2019)	Harmful
Rhodosporidiobolus fluvialis	Yeast capable of synthesizing lipids for biofuels (Polburee & Limtong, 2020)	Neutral
Rhodotorula mucilaginosa	Known infectious agent in humans (Wirth & Goldani, 2012)	Unknown
Thielavia terrestris	Tolerates high temperatures and low pH; other fungi in the genus endophytic, pathogenic or neutral (Tõlgo et al., 2021)	Mixed
Tomentella stuposa	Ectomychorrizal, (Jakucs et al., 2005)	Beneficial
Trichoderma virens	Increase biomass production and lateral root development (Contreras-Cornejo et al., 2009)	Beneficial

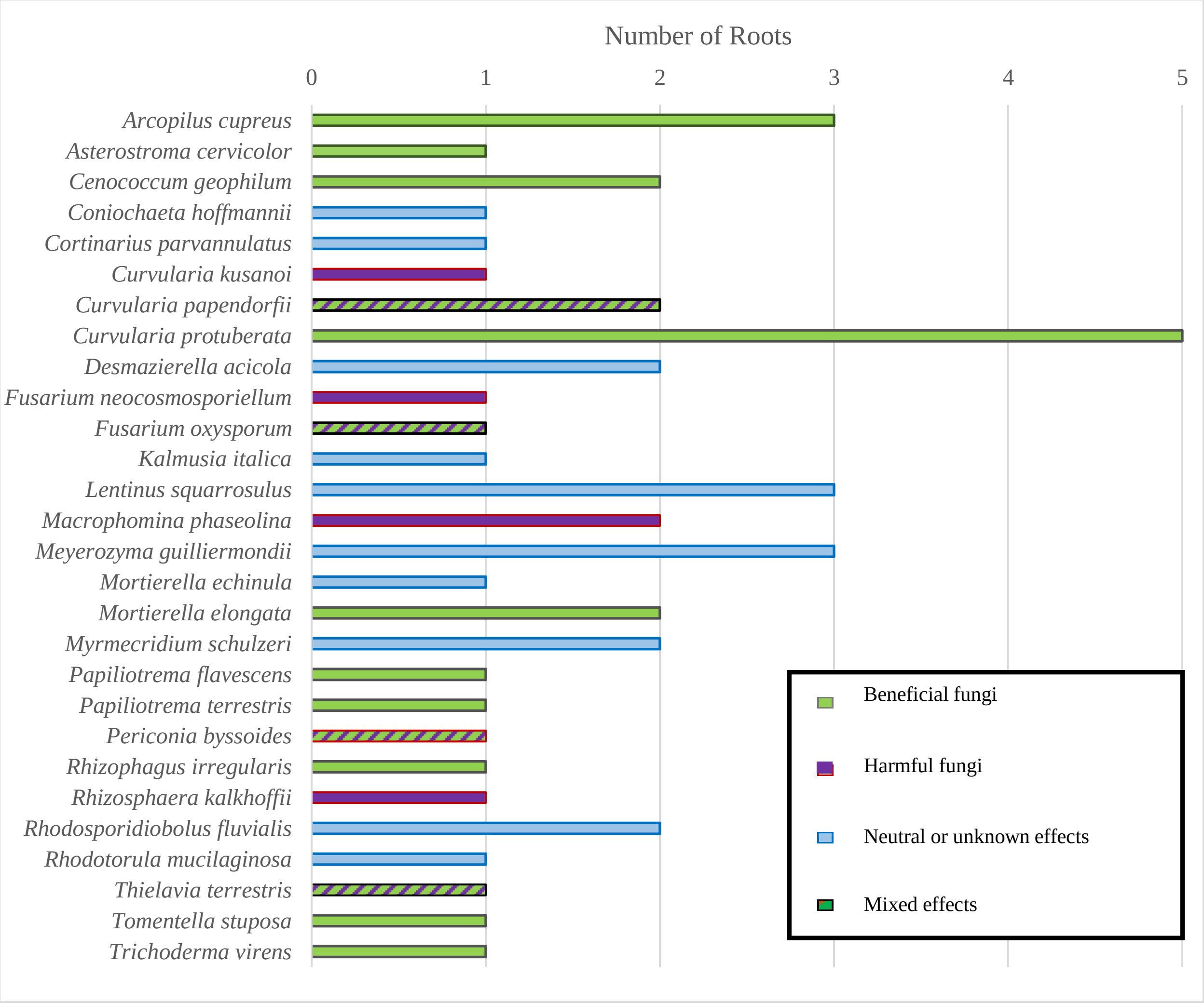


Figure 13. Number of root samples with fungal species present. This chart shows the occurrence of the 28 species of fungi identified in Schwalbea roots. The Y-Axis corresponds with number of roots in which each species was present. The bars are color-coded to correspond with the action of these fungi on plants: beneficial, harmful, neutral, or mixed. C. protuberata was most common, occuring in five roots, or approximately 30% of the roots sampled.

2.4 Discussion

Since Kelly & Denhof (2022) found significant differences in soil carbon, moisture, and pH inside and outside of Schwalbea populations, it was expected that similar trends might be observed in this study. The results presented here, however, indicate that there are no significant differences between soils within Schwalbea populations and soils upslope of or between populations. These data suggest that soil properties are not a discriminating factor among Schwalbea populations, at least in the southeastern extent of the range (see Kelly, 2006 and Kelly & Denhof, 2022 for descriptions of microsite requirements for Schwalbea in New Jersey). This suggests that edaphic conditions don't appear to be limiting the spread or survival of outplanting beyond the current spatial boundaries of existing populations. It could mean that the soil characteristics measured here are not critical to consider in selecting sites for outplanting and in searching for new populations. However, soil moisture was not measured in this study because of the lack of sensitivity in the available moisture meter and prolonged drought at the time of sampling, so this difference remains untested in the southern portion of the range. With the effects of climate change amplifying drought events, it could be important to assess possible moisture requirements of the species. Since no significant effects were found here in terms of soil characterizations, additional limitations to Schwalbea establishment should be researched. What is preventing populations from spreading to new locations?

Because heterogeneity in soils is strongly associated with species richness in plant communities (Vivian-Smith, 1997; Williams & Houseman, 2013; Wilson, 2014; Xue et al., 2019), it is interesting that the soil measured in this study was quite similar across groups. Long-term, regular soil measurements are not available for the populations studied here, so it is unknown whether soil properties might have changed over time. However, due to the effects of climate change, prolonged periods of drought and high temperatures are more likely across Schwalbea's range. In 2022, 100% of Baker County in Georgia, where the Schwalbea populations studied here exist, experienced abnormally dry conditions or moderate drought for at least ten months of the year (Georgia Drought Monitor, 2022). These changes could have impacts on soil structure and nutrient mobility that in turn affect niche availability. It is possible that microsite specifications do exist, as they seem to in the northern portion of the range, but were not reflected here due to changing soil conditions. On the other hand, it is possible that there are limiting factors other than soil properties that most influence the distribution of Schwalbea. Longleaf forests are places of high diversity when managed well with fire, and factors not measured here such as light availability, soil disturbance, and leaf litter (Kirkman, 1998), could be more critical in this part of

Schwalbea’s range than soil factors. Perhaps soil microsite differences are more important in New Jersey, where fire has not historically been a part of the population’s management (Kelly, 2006).

Soil pH exhibited moderate variation across the sample sites, and this was not at the level of statistical significance (although, see Chapter 3 for a more extensive analysis of pH). Another possibility for the lack of observed differences is that the soil samples collected from inside populations at Ichauway were not taken from close enough to actual Schwalbea individuals to register fine-scale differences, which can occur on a 1-3 cm scale (Vivian-Smith, 1997) or that soil categories were miscategorized. Kelly (2006) noted that clusters of Schwalbea had been obscured in the New Jersey populations until a large population boom resulted in enough individuals for the spatial clustering to become apparent. Kelly also utilized extensive yearly Schwalbea data to flag points known to have supported Schwalbea from 1999 - 2006, when the study occurred. This ensured an accurate representation of the Within Schwalbea areas. This detailed level of data is not available for the Ichauway populations. With the capacity for prolonged dormancy in Schwalbea, it is possible that soils collected from the areas labeled Upslope or Between in this study might more correctly have been described as Within soils if there were Schwalbea growing therein that were not visible aboveground at the time of sampling.

Silt, sand, Al, Cr, Fe, Mg, Mn, and S all exhibited differences across individual populations, although not on a microsite scale. Perhaps Schwalbea can tolerate a range of values in these particular soil characteristics; thus, they are not limiting Schwalbea’s distribution. More research is necessary to determine whether the levels of the soil properties that did not change across sites are essential levels for Schwalbea, or if the range of possible values is simply limited by the study area itself (e.g., perhaps the range of Zn values at Ichauway does not substantially vary between 2.5 and 4.8 across sites).

The present study found Schwalbea roots to contain a diversity of fungi, including potential pathogens and symbionts. Since none of the fungal strains found occurred in all, or most, of the roots sampled, it is difficult to make conclusions about the nature of the relationships. However, de Freitas et al. (2018) point out that the capacity for communication between a fungus and a plant is a prerequisite for interactions, and since fungi were in fact present in the roots, the mechanisms for fungal-plant relationships are in place in this natural population of Schwalbea. How prevalent these relationships are in all Schwalbea is unknown, and further research is required to build a better understanding of the fungal dynamics at play here.

Because roots were only sampled from the most vigorous individuals in one population of Schwalbea to reduce inflicting harm, certain dynamics remain unclear. Do all Schwalbea form relationships of some kind with fungi? Are those genera and species that were found in the samples present in less vigorous individuals as well? Is the presence of harmful fungi mediated by beneficial genera and species? Is the presence of beneficial fungi in 9 out of 17 roots sampled involved in the observed vigor of these plants? On the other hand, could the harmful fungi observed play a role in the rarity of the species? There was also an abundance of both undescribed fungal and non-fungal DNA in these roots. Most of this DNA was presumably Schwalbea DNA, and some was most likely bacterial, which was not sequenced here but is abundant in soil. What might the role of bacteria be in Schwalbea's life cycle? It is known that some species of fungi, such as *Mortierella elongata*, house bacteria in their cells, a process by which they are thought to influence the growth of plants positively (Sato et al., 2010). It is possible that bacteria, fungi, and Schwalbea could form important relationships that were not explored here.

Some of the fungal genera found are either ectomycorrhizal or saprophytic. Because ectomycorrhizal fungi (ECM) most commonly associate with woody species and saprophytes decay dead material, this might indicate that these fungal strains were not in fact colonizing Schwalbea roots but were instead present as spores, or that part of some roots sampled were actually dead. However, there are cases when ectomycorrhizal fungi are symbiotic with herbaceous plants (Massicotte et al., 1998; Dickie et al., 2004; Gao & Yang, 2016; Hoeksema et al., 2018; Thoen et al., 2019). Species from the genera *Cenococcum, Amanita, and Inocybe*, which were found in Schwalbea roots here, were found to be ectomycorrhizal with the herbaceous perennial *Bistorta vivipara* L., a plant in the family Polygonacea which grows in the Arctic (Massicotte et al., 1998). Species in the genus *Cortinarius*, also found here, are known to be ectomycorrhizal with trees, shrubs, and herbs (Xie et al., 2020). Hess & Pringle (2014) point out that the lineage of ectomycorrhizal fungi goes back to saprotrophic fungal ancestors, and that ECM evolved multiple times independently of each other. Thoen et al. (2020) describe species in the genus *Mycena* who exist on a continuum of saprotrophy and biotrophy, capable of both decomposing organic matter and forming endophytic relationships with plants. Many of the genera found in Schwalbea roots contain species that are both saprophytic, endophytic, and even parasitic. Given that scientists have only described approximately 150,000 species in a Kingdom estimated to contain anywhere between 2.2 and 13.2 million species, much is left to learn about the diversity of this group of organisms and the versatile ways they are capable of interacting with plants (Hyde, 2022). These interactions are also continuing to evolve.

While soil conditions were not found to strongly differ between categories of Schwalbea presence and absence in this study, interesting fungal relationships were indicated. It is possible that one limiting factor in Schwalbea distributions might be the community of fungi present in the rhizosphere. Jacquemyn et al. (2014) found fine scale differences among rhizosphere fungal communities in co-occurring orchids. Rasmussen et al. (2018) found distinctive communities of arbuscular mycorrhizal fungi (AMF) across distances as little as 30 cm. These fungi were also found to respond differently to changes in moisture, pH, and temperature. Higher temperatures in their study led to less diversity of fungi. AMF fungi also respond differently to increased allocations of carbon from their plant hosts, with some unable to make effective use of more resources (Bever et al., 2001). Changes in fungal communities are thus increasingly likely under climate change, and these changes are likely to elicit and be influenced by changes in plant communities as well. This exploration of Schwalbea’s fungal ecology stresses the need for further studies to elucidate the role of fungal relationships in hindering or protecting Schwalbea.

Chapter 3: Indicator species analysis and pH requirements for *Schwalbea americana*

3.1 Introduction

A primary goal of ecologists is to describe communities across the globe and to understand the linkages between the species occurrences therein and environmental conditions (Dufrene & Legendre, 1997; Diekmann, 2003; Dengler et al., 2011). Vegetation classification can influence applied conservation by, for example, determining what lands get protection (Delaroche et al., 2022). Another application of vegetation classification is identifying bioindicators within communities that can aid scientists in monitoring the health or degradation of a system (Košuthová & Šibík, 2013; Kolon et al., 2015; Terwayet Bayouli et al., 2021; Chaplygin et al., 2022). The presence or absence of particular species can be indicative of changes unapparent to the naked eye otherwise. An entire journal, *Ecological Indicators*, is dedicated to the topic. Of interest here is the ability to translate data about rare plant community composition and environmental measurements (namely, pH) into meaningful conservation of the endangered hemiparasite *Schwalbea americana* (Schwalbea). Indicator Species Analysis, Functional Group analysis, and pH comparisons among groups will be explored in the present chapter.

Indicator species are defined as those species that are most characteristic of a particular group, occurring mostly in that group and in most sites belonging to that group (Dufrene & Legendre, 1997). Analysis of such species contributes to conservation efforts, land management, and rare species and habitat monitoring. It has been used to describe plant communities along vegetational and environmental gradients (Khan et al., 2016; Chytry et al., 2020; Friday & Scasta, 2020) as well as to identify plant affiliates of rare species (Kintsch & Urban, 2002; Baumberger et al., 2012). Bioindicators are at present indispensable in the field of conservation. Among the reasons that Zonneveld (1983) describes for this are: (1) plants are manifestations of unseen cumulative processes that can be revealed through the presence of particular species or plant groups but might require extensive, repeated measurements of multiple variables to reveal otherwise, and (2) the tools required to measure these unseen processes are often prohibitively expensive and require ample time for repeat measurements. In a world where species are being lost at unprecedented rates, tools for bioindication such as indicator species are crucial aids in the urgency of conservation.

Dufrene and Legendre (1997) developed a technique to identify indicator species using an Indicator Value (IV). This approach does not rely on the abundances of other species sampled to assign an IV to each species as earlier techniques like TWINSPAN do, making it a strong tool for examining each species individually (de Caceres et al., 2010). An IV is computed by multiplying (A) the mean abundance of a species, *i*, in a particular group of sites, *j*, as compared to its abundance in all other sites and (B) the number of sites in group *j* occupied by species *i* compared to the total number of sites in group *j* (Dufrene & Legendre, 1997). Thus, IV takes both constancy and fidelity into account when examining a species' distribution. Ultimately, the IV is not weighted by its absolute value but by the difference between IV's for the groups under inspection (Peck, 2016). Dufrene and Legendre's method also enables the researcher to define the site groupings based on ecological factors, such as the presence of a rare species. Such groupings might not be identified by ordination techniques such as Canonical Correspondence Analysis (CCA) or Nonmetric Multidimensional Scaling (NMS), which seek a strong main gradient to organize sites by. Such a gradient is unlikely to be the secondary or tertiary gradient upon which the distribution of a rare species might depend and so might miss the patterns in question.

Identifying the species that co-occur with an endangered species, such as Schwalbea, can aid conservationists in identifying suitable habitat for outplantings and locating new populations (Baumberger et al., 2012). Researchers know that Schwalbea is predominantly found in ecotones between wetlands and upland pine savannas, but specific species associated with Schwalbea populations have only been described in the literature in New Jersey (Kelly, 2006; Kelly & Denhof, 2022). Knowing this type of information in parts of the southern extent of Schwalbea's range could give plant ecologists an additional search image in the field when surveying for suitable habitat and new populations.

Kelly & Denhof (2022) also examined differences in functional group composition between adjacent communities with and without Schwalbea present. Plant functional groups are defined as "non-phylogenetic groupings of species which perform similarly in an ecosystem based on a set of common biological attributes. They can be defined in relation to either the contribution of species to ecosystem processes (such as carbon or water cycling) or the response of species to changes in environmental variables (such as climatic variables or disturbance)" (Lavorel et al., 1997, p. 475). Examples of functional groups are specific floral designs, life strategies, and growth forms. The assemblage of plants of various functional types is an important indicator of the ecology of a habitat since they are linked to invisible, difficult-to-measure characteristics such as soil microbiology (Zhang et al., 2011). Functional type assemblage is also useful in predicting the survival of a given plant community after disturbance (Noble & Gitay, 1996; Lavorel et al., 1997; Franks et al., 2009) and is helpful in monitoring rare species (Rossell & Losure, 2005). Changes in functional group composition could indicate the need for changes in management. For instance, percent cover of woody species in a fire-maintained habitat could be indicative of the need for more or less fire. This study seeks to understand whether a particular assemblage of functional groups identified by growth form and wetland indicator status is associated with Schwalbea populations.

Lastly, this study addresses the question of whether the presence of Schwalbea is limited by pH. Soil pH is well-known to affect plant community composition and species richness (Merunková & Chytrý, 2012; Michaelis et al., 2016). It is particularly influential in the distribution of rare plants (Wieger Wamelink et al., 2014; Nielsen et al., 2020). Kelly & Denhoff (2022) found significant differences in pH between Schwalbea populations in New Jersey and adjacent uplands and lowlands, with Schwalbea soil pH being slightly higher than surrounding soils. Does this pattern hold in southern portions of the species' range?

In summary, this chapter addresses the following questions: Are there certain species that indicate the presence of Schwalbea? Are there particular functional group assemblages that are associated with Schwalbea populations? Are there differences in pH between Schwalbea presence and absence sites? It is hypothesized that there will be differences in pH between soils with and without Schwalbea.

3.2 Site and Methods

Ichauway is a 12,000+ hectare (nearly 30,000-acre) ecological reserve consisting of myriad longleaf pine communities, from depressional wetlands to hardwood hammocks to shrub-scrub and pine savanna uplands. It is in Baker County in SW Georgia in the Dougherty Plain, an area with karst topography, and is mostly composed of sandy soils. The Schwalbea populations here occur in ecotones between seasonally inundated wetlands and upland longleaf savannas. They are referred to here as Rhexia 1-4, Pond 32, Parmalee, and Jericho. Their soils are "transitional between poorly-drained sandy clay loams of adjacent wetlands and well-drained loamy sands or sandy loams of adjacent uplands," (Kirkman, 1998, p. 117). Populations are burned at least every other year (Appendix Table A6).

Each of the Schwalbea populations' boundaries has been mapped in ArcGIS. Pond 32 and Jericho are each composed of only one distinct population. Parmalee is composed of two subpopulations, but one of these contains less than ten individuals so it was not included. Rhexia consists of four subpopulations.

To create grids from which to randomly sample vegetation inside and outside Schwalbea populations, Schwalbea polygons were imported into QGIS. The Vector - Research Tools - Create Grid tool was utilized to create grids of 0.25 m^2 plots over the polygons, and these were clipped to fit each polygon's extent. This process created grids of Inside-Schwalbea plots. This grid was then buffered by 2 meters to account for possible dormancy in Schwalbea that could result in unrecorded Schwalbea presence outside the polygons.

To create Outside-Schwalbea plots, a large bounding rectangle was built around each buffered Schwalbea polygon with the smallest possible length and width that would encompass the entire polygon + 2 m. Because each subpopulation is a different size, the final bounding rectangle was different for each subpopulation. Jericho is bounded by a 20 x 20 m rectangle. Parmalee's bounds are 15 x 15 m. Pond 32 is bounded by a 15 x 10 m rectangle. Rhexia 1 is bounded by a 30 x 30 m rectangle. Rhexia 2 is composed of two subpopulations whose Outside plots overlap, one 20 x 20 m and the other 10 x 10 m (Fig. 14). Rhexia 3 is bounded by a 35 x 50 m rectangle. Rhexia 4 is also composed of two rectangles that overlapped and were thus combined into a single subpopulation. One of these bounding rectangles is 15 x 20 m, and the other is 10 x 10 m.

After constructing the bounding rectangles, grids of 0.25 m^2 plots were created over them. The Vector - Geoprocessing Tools - Symmetrical Difference tool was then utilized to remove the Inside plots and 2 m buffer, thus creating the Outside plots.

The Vector – Research Tools – Random Selection tool was then used to randomly select 5% of the plots from both the Inside and Outside groups, resulting in the selection of 10 plots at Pond 32, 20 plots at Parmalee, 48 plots at Jericho, 78 plots at Rhexia 1, 20 plots at Rhexia 2, 166 plots at Rhexia 3, and 34 plots at Rhexia 4.

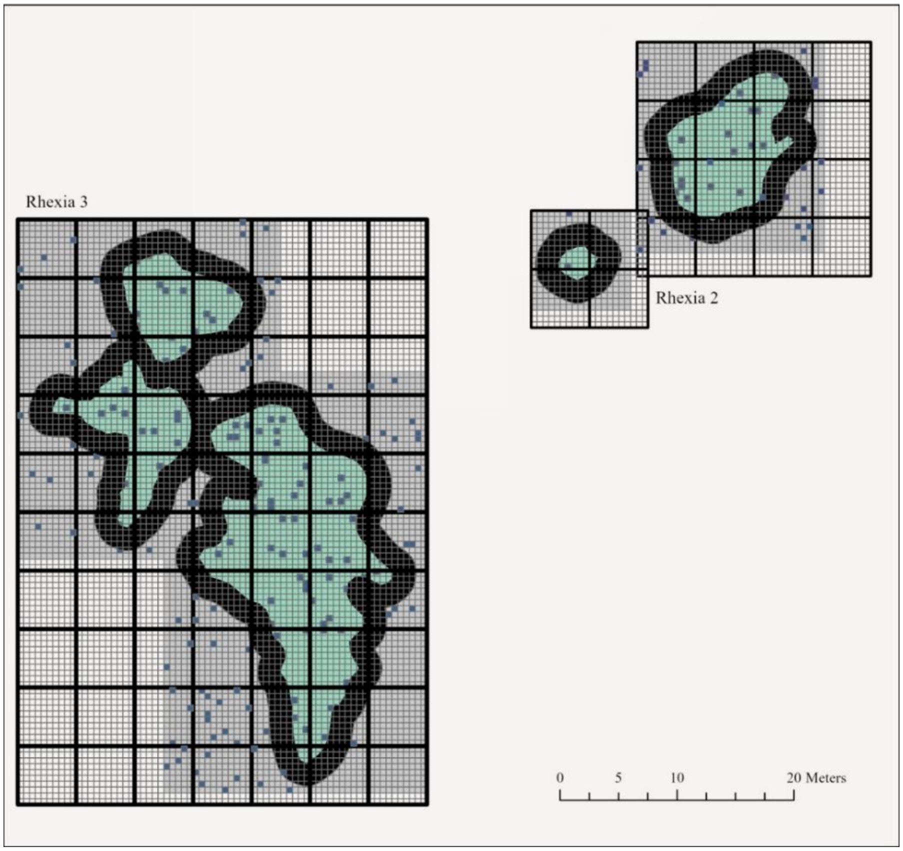


Figure 14*. *Vegetation sampling layout at sites Rhexia 2 & 3. Inside plots are in green, with selected plots in dark blue. Outside plots are in gray, with selected plots in dark blue. The 2-meter buffer is black. To create a rectangular bound that could easily be set up in the field, extra area was often included. This excess area is light tan and was left out of plot selection.

To sample the plots, 0.25m^2 frames were set up in the field after demarcating each bounding rectangle using a GPS, compass, and measuring tapes. It was ensured that no Outside plot was within 2 meters of Schwalbea. Species' abundances and bare ground were recorded in each plot by assigning a percent cover value from 0.5-100. The combined values could exceed 100 due to vegetation overlap. Species were identified according to Weakley's Flora (2020) in the field and in the Plant Ecology lab at Ichauway. Unknown species were pressed for subsequent identification and ultimately stored in the herbarium.

To examine functional group assemblage, each species recorded in the field was assigned to two classifications. One functional group classification is growth form. Species were classified as a Forb-Aster, Forb-legume, Forb-other, Graminoid, Shrub, Subshrub, Tree, or Vine. This information was obtained from a Plant Attribute List maintained by the Plant Ecology Lab at Ichauway and based on the USDA PLANTS Database (2023). The decision to include subsections of the Forb group was made since Asters are biologically significant to Schwalbea and Legumes are large components of longleaf communities. Kelly (2006) also utilized these categories. Schwalbea grown with Asters had higher survivability in a study by Kelly & Denhof (2022) than those grown with other vegetation types. Asters are also known hosts for Schwalbea (Helton et al., 2000; Kelly, 2006; Kelly & Denhof, 2022). The second functional group classification is Wetland Indicator Status: is the species classified as Facultative (equally upland and wetland), Facultative Upland (mostly upland), Facultative Wetland (mostly wetland), Obligate Wetland, or Upland. These assignments were made according to the National Wetland Plant List, which also informs the USDA PLANTS Database (U.S. Army Corps of Engineers, 2020). When a species was not documented in the list, its status was determined by referencing Weakley's Flora (2020) for habitat characteristics. Unclassified species were typically upland species or had recently undergone taxonomic revisions.

To measure pH, tools that could be used in the field were sought rather than taking soil samples from every plot. This was to minimize disturbance to Schwalbea habitat. Hanna Instruments' GroLine Professional Portable Soil pH Meter, with a sensitivity to the thousandth unit, was utilized to measure pH at each plot. A small hole between 10 and 15 cm was dug using a weeding tool in the center of each plot. Because of an unusually dry season in summer and fall of 2022, a few drops of deionized water were added to each hole. The pH meter was then inserted, and the auto-stabilization button was activated to stop the meter once the pH recording had stabilized. The readings were recorded and transferred to Excel.

Data Analysis

Vegetation data was entered into Excel and processed in R (R Core Team, 2022) using the dplyr, xlsx, and tidyverse packages. Data was further shaped according to the requirements of PC-ORD Version 7 (McCune & Mefford, 2016). A total of 400 plots were recorded, more than the original expectation of 396, due to four extra plots unintentionally being set up in the field. The decision was made to exclude all the Jericho plots from the final analyses, because this site had not been burned the same year as field work occurred and thus had a quite different floristic composition than other sites. Unburned sites are much shrubbier than burned sites and contain species that are not characteristic of the healthy ecosystem (Kirkman, 1998). Outlier analysis conducted in PC-ORD supported this decision since over 16% of Jericho plots were identified as outliers. Ten additional plots identified as outliers were also removed after further investigation. These all occurred at Rhexia and occurred right along the borders of the Inside-Outside divide, making it likely that they were more closely related to the opposite category from which they were classified. Three plots identified as outliers were retained. One was kept because it contained Schwalbea, and so the community there was important to consider. Another was retained because it occupied a central position in its category rather than an edge position. A third was kept because it was one of only ten plots at Pond 32.

After removing outliers and Jericho, 342 plots remained for analysis. Two hundred and eighteen species were documented, but data-set rare species that occurred in less than three plots were removed along with the bare ground measurement, leaving 105 species in the analysis. This helped reduce the percentage of zeroes included in the data, which can make interpretation of messy species datasets easier (McCune & Grace, 2002; Peck, 2016). Data was modified by first blocking by site and then relativizing by the maximum observed cover for each species. This relativization was selected to down-weight the influence of species whose cover values might have been larger simply because of their functional form or temporal growth cycle. While achieving better balance in species data, this technique maintains the relative cover relationships between species and plots. Blocking by site was performed to account for site-specific limits on species cover.

Each of the 342 remaining plots was classified in three ways (see Fig. 15): (1) Inside or Outside, (2) Schwalbea Presence or Absence, and (3) Inside-Presence or Inside-Absence. Indicator Species Analysis was conducted in PC-ORD Version 7 and examined indicator species for each of these classifications. Dufrêne & Legendre's (1997) method was used for calculating the Indicator Values. A randomization test was run with 10,000 iterations to calculate p-values based on the proportion of randomization trials with indicator values equal to or exceeding the observed value.

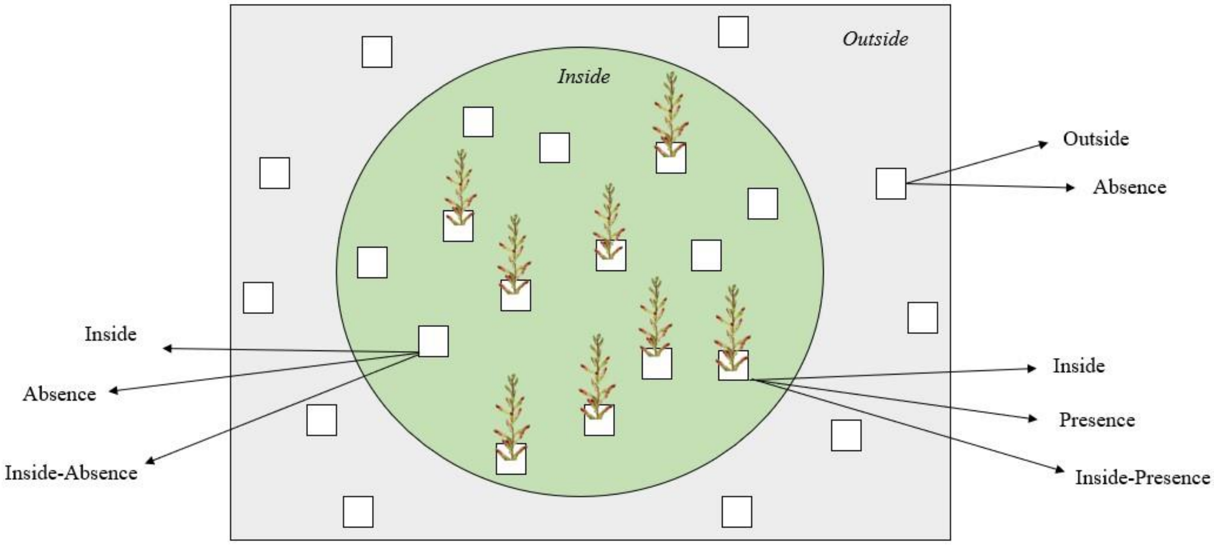


Figure 15*. *Diagram of plot classifications. Outside plots could only be assigned to two of the categories, Outside (vs. Inside) and Absence (vs. Presence). Inside plots could be Inside (vs. Outside), Presence or Absence, and Inside-Presence or Absence.

Functional Group and pH were analyzed in R. A Shapiro-Wilk test was used to test normality in datasets. A Levene test was used to test for variance equality. Differences in pH were assessed using either a t-test when variance was equal between groups compared or a Welch's t-test when variance wasn't equal. pH data was normally distributed. When variance was equal, a one-way ANOVA test was used to compare means across sites. When variance was unequal, Welch's ANOVA was instead used. To test pairwise differences across sites, a Games-Howell test was used since site sample sizes were unequal. Adjustments for nonnormal data were used to compare means for functional group composition across categories and sites. Instead of t-tests, Wilcoxon tests were used to compare means across categories. Kruskal-Wallis tests were used to compare means among sites, followed by Games-Howell pairwise tests.

3.3 Results

Indicator Species Analysis

A total of 218 species were identified across all vegetation plots (see Appendix Table A5 for a complete list). For the Inside and Outside groups, 18 indicator species were found with $p < 0.01$ (see Table 5). This threshold was chosen because when using an alpha of 0.05, the expected number of indicator species found at random was over 10% of the actual number found. When using an alpha of 0.01, the expected number of indicator species was less than 10% of the actual. Eleven species were indicative of the Inside group, and seven were indicative of the Outside group. Four graminoids, six forbs, and one shrub were indicators of the Inside group. Two of these are known Aster Schwalbea hosts, and one is another Aster. Two graminoids, two vines, one fern, one tree, and one forb were indicators of the Outside group. For the Schwalbea Presence and Absence groups, 10 species were found to be indicative of the Presence Group (See Table 6). Again, the 0.01 p-threshold was used. No species other than Schwalbea itself were found to be indicators for either the Inside-Presence or Inside-Absence group.

Table 5. ISA analysis (Inside-Outside groups). Species that were found to be strongly indicative of particular groups.

Species Code	**Species Name**	**Group affiliated with**	**Observed Indicator Value (IV)**	**p**
ARBE	*Aristida beyrichiana* Trin. & Rupr.	Inside	52.4	< 0.001
CHMA	*Chrysopsis mariana* (L.) Elliott	Inside	26.6	< 0.001
DIST	*Dichanthelium strigosum* (Muhl. ex Elliott) Freckmann	Inside	47.9	< 0.001
DITN	*Dichanthelium tenue* (Muhl.) Freckmann & Lelong	Inside	56.2	< 0.001
HYSU	*Hypericum suffruticosum* W.P. Adams & Robson	Inside	22.0	< 0.001
LE01	*Lechea* sp. L.	Inside	42.8	< 0.001
PI01	*Pityopsis* spp.*	Inside	56.9	< 0.001

RH01	*Rhynchospora* sp. Vahl	Inside	34.6	< 0.001
SYAD	*Symphyotrichum adnatum* (Nutt.) Nesom	Inside	38.2	< 0.001
TRSM	*Tragia smallii* Shinners	Inside	18.2	0.002
XYCA	*Xyris caroliniana* Walter	Inside	5.6	0.007
ARG1	*Aristida* sp. L.	Outside	7.1	0.002
IPPA	*Ipomoea pandurata* L.	Outside	11.1	0.002
KEVE	*Kellochloa verrucosa* (Muhl.) Lizarazu, M.V. Nicola, & Scataglini	Outside	5.8	0.001
PTPS	*Pteridium pseudocaudatum* (Clute) Christenh.	Outside	41.5	< 0.001
QUGE	*Quercus geminata* Small	Outside	5.3	0.003
SMBO	*Smilax bona-nox* L.	Outside	5.3	0.01
SOVR	*Solidago virgata* Michx.	Outside	13.8	< 0.001

* *Pityopsis* species identified only as PI01, because species-level identification was impossible at time of sampling without flowers. Subsequent field identification revealed both *P. nervosa,* (Willd.) Dress and *P. graminifolia,* (Michx.) Nutt. to be present in plots for both groups and at all sites.

Table 6. ISA analysis (Presence-Absence Groups). All reported species were found to be indicative of the Presence group. Those species which were not also found to be indicators of the Inside-Outside groups are in bold.

Species	**Species Name**	**Observed Indicator Value (IV)**	**p**
ARBE	*Aristida beyrichiana* Trin. & Rupr.	57.1	< 0.001
CHMA	*Chrysopsis mariana* (L.) Elliott	29.0	0.002
DIST	*Dichanthelium strigosum* (Muhl. ex Elliott) Freckmann	44.7	0.003
DITN	*Dichanthelium tenue* (Muhl.) Freckmann & Lelong	52.6	< 0.001
DYOB	*Dyschoriste oblongifolia* (Michx.) Kuntze	46.2	0.008
LE01	*Lechea* sp. L.	39.7	< 0.001
PI01	*Pityopsis* spp.*	54.5	< 0.001
RH01	*Rhynchospora* sp. Vahl	36.7	< 0.001
SCTE	*Schizachyrium tenerum* Nees	42.6	< 0.001
SYAD	*Symphyotrichum adnatum* (Nutt.) Nesom	38.0	0.003

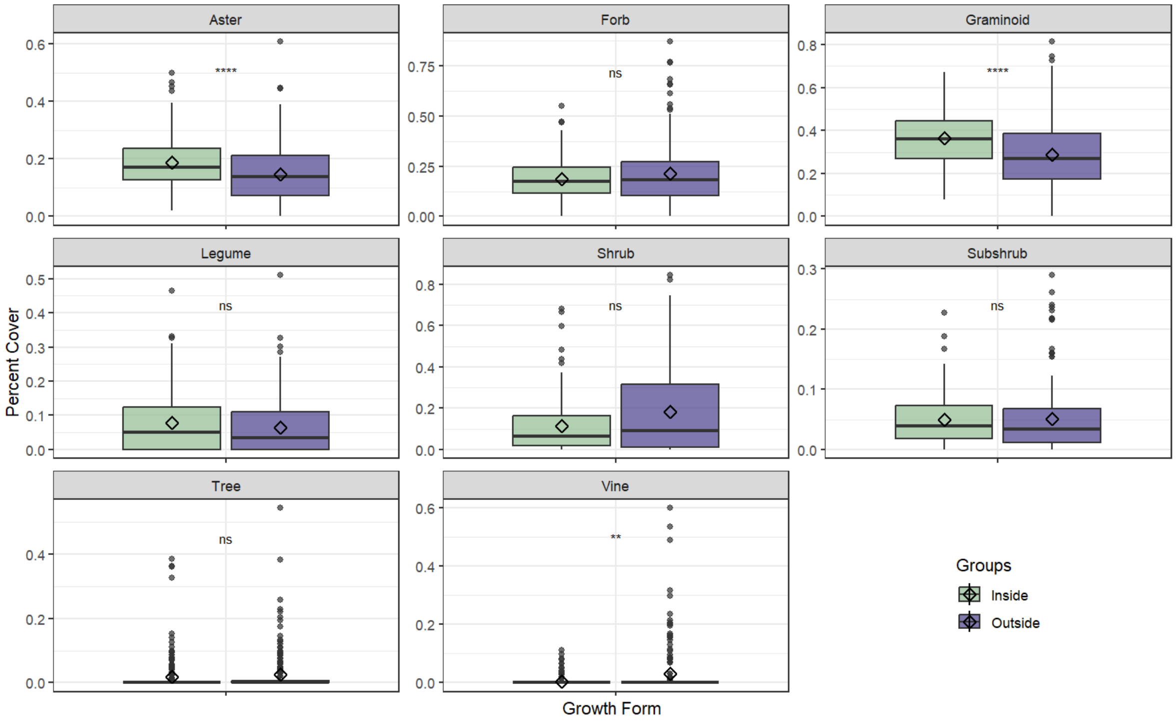
Functional Groups

Functional group cover was significantly different across groups. Inside plots had significantly more graminoid cover, Z = 4.247, *p* < .001, and Aster cover, Z = 3.066, *p* = .001, than Outside plots (Fig. 16a). Inside plots had less vine cover, Z = 2.689, *p* = .004 (Fig. 16a).

Absence plots had more vine cover, Z = 1.678, *p* = .047 than plots with Schwalbea (Fig. 16b). Presence plots had more graminoid cover, Z = 3.309, *p* < .001 and forb cover, Z = 2.506, *p* = 0.006 than

Absence plots (Fig. 16b). No difference was observed between Inside-Outside groups or between Presence-Absence groups in bare ground, legume, shrub, subshrub, or tree composition.

When examining functional group differences between Inside-Presence and Inside-Absence groups, Inside-Presence plots had significantly more forb cover than Inside-Absence plots, Z = 3.102, $p < 0.001$ (Fig. 16c). Inside-Absence plots had more aster, Z = 2.179, $p = 0.015$ (Fig. 16c) and subshrub cover, Z = 1.965, $p = 0.025$ than the Inside-Absence group (Fig. 16c).



(a)

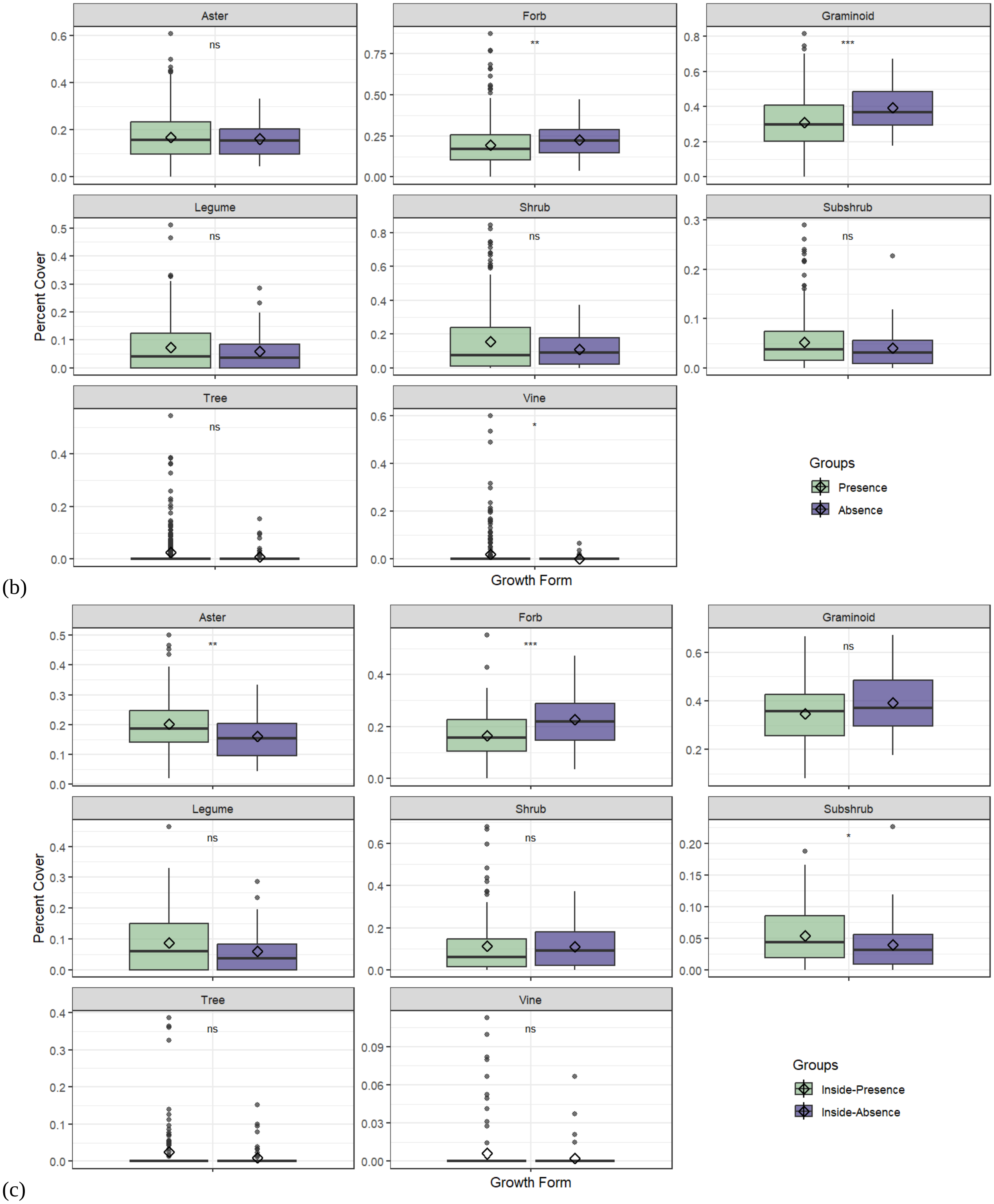
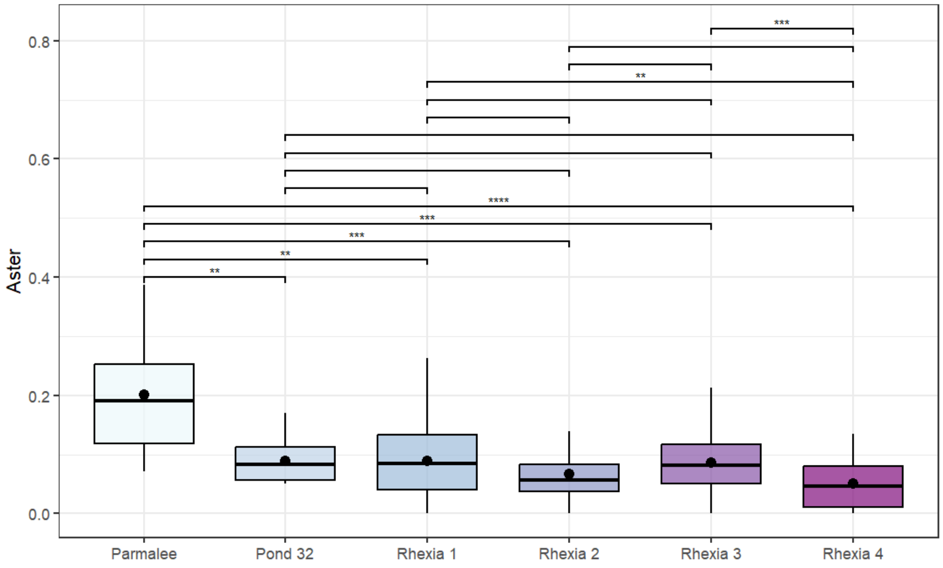
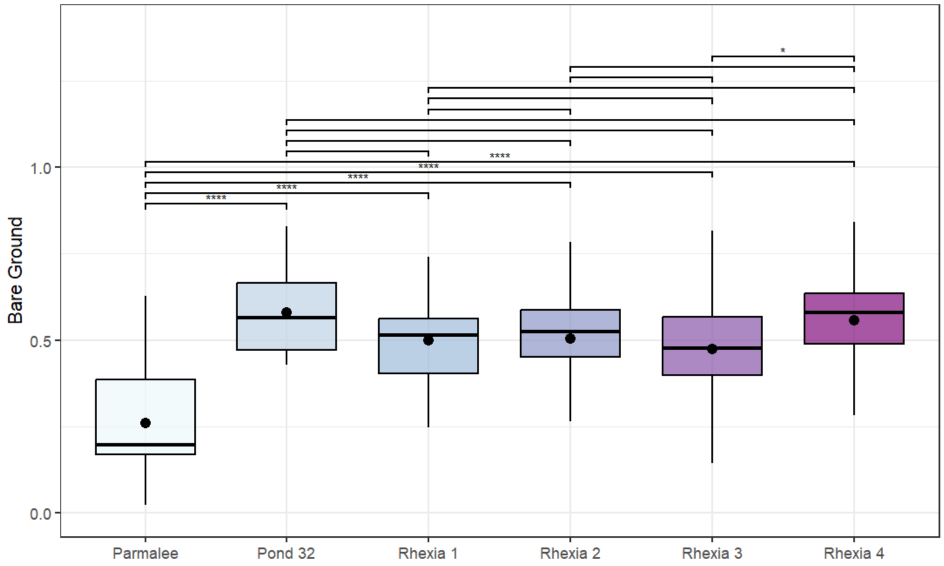


Figure 16. ***Differences in functional group composition between Inside and Outside groups.***

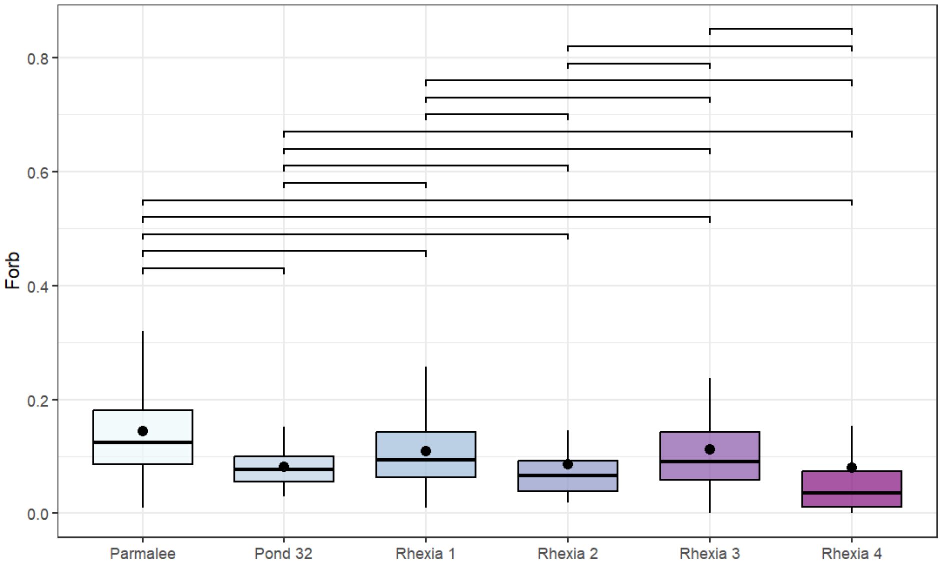
There were significant differences across sites in functional group cover. Parmalee had significantly more aster cover than any other site, and Rhexia 1 had more than Rhexia 4 (Fig. 17a). Parmalee had significantly less bare ground than any other site (Fig. 17b). There was no difference in forb cover (Fig. 17c). While graminoid cover was similar across Parmalee, Pond 32, and Rhexia overall, it differed between individual Rhexia sites (Fig. 17d). Rhexia 1 had less graminoid cover than Rhexia 2 and Rhexia 3. Rhexia 2 and Rhexia 3 had more graminoid cover than Rhexia 4. Parmalee had more legume cover than every site except Rhexia 3 (Fig. 17e). Rhexia 2 and 3 had more legume cover than Rhexia 1 and 4. Rhexia 4 had more shrub cover than every site except Rhexia 1 (Fig. 17f). Rhexia 1 had more shrub cover than all sites except for Rhexia 3 and Rhexia 4. Parmalee and Pond 32 had less shrub cover than the other sites. Parmalee had more subshrubs than any site except Rhexia 4 (Fig. 17g). Pond 32 had less tree cover than any site except Parmalee and Rhexia 4 (Fig. 17h). Parmalee, Rhexia 1, and Rhexia 2 had significantly more vine cover than Rhexia 3 and Rhexia 4 (Fig. 17i).


***
**
****
***
***
**
**
Aster
0.0
0.2
0.4
0.6
0.8
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

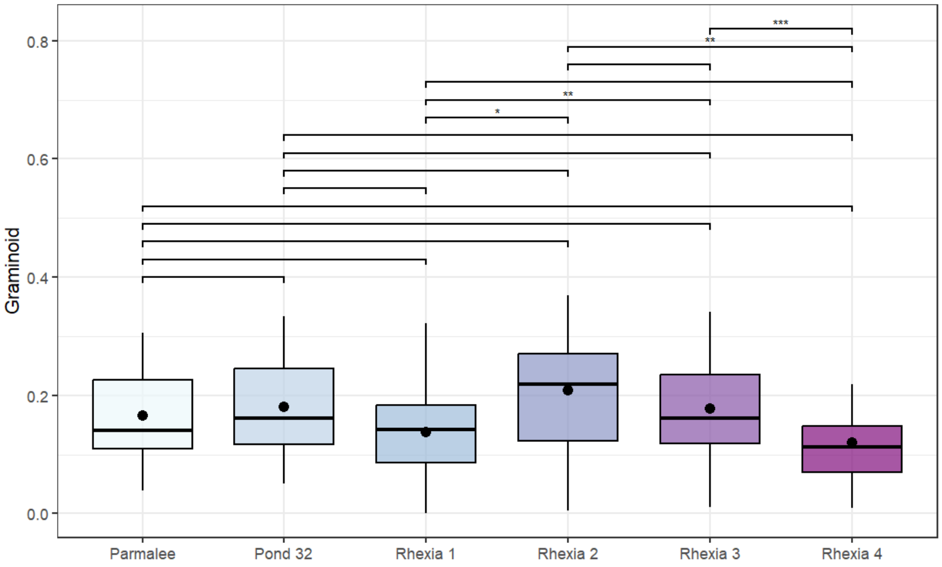
(a)


*
****
****
****
****
****
Bare Ground
0.0
0.5
1.0
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

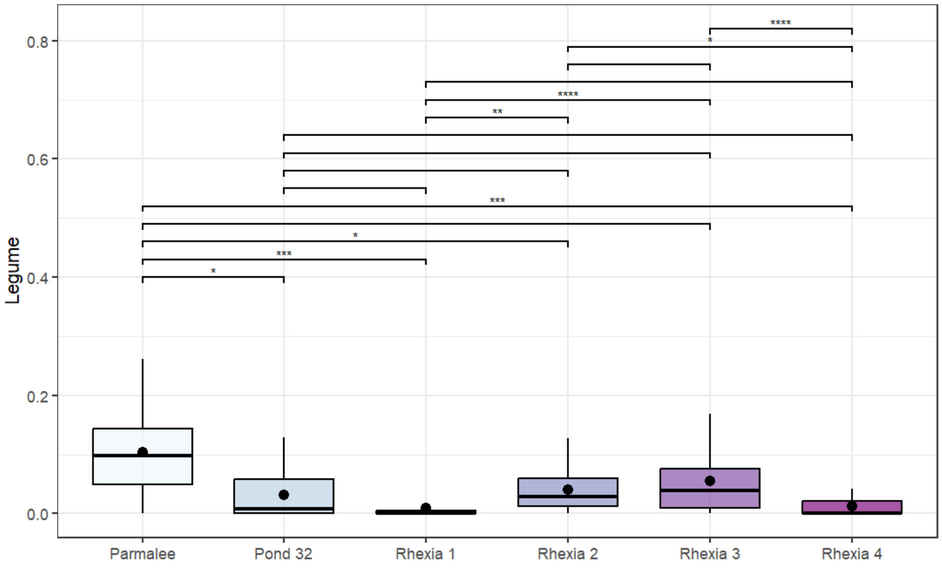
(b)


Forb
0.8
0.6
0.4
0.2
0.0
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

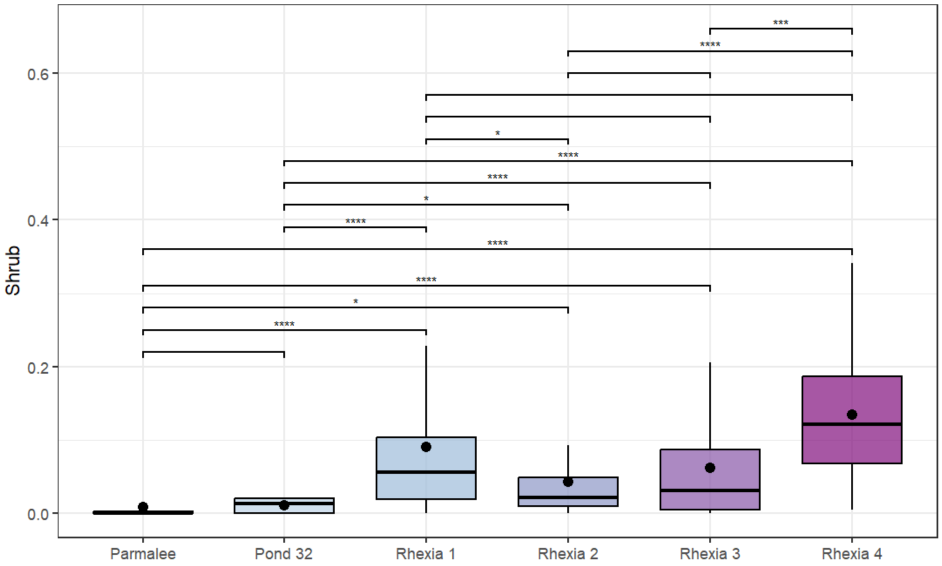
(c)


Graminoid
***
**
**
*
0.8
0.6
0.4
0.2
0.0
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

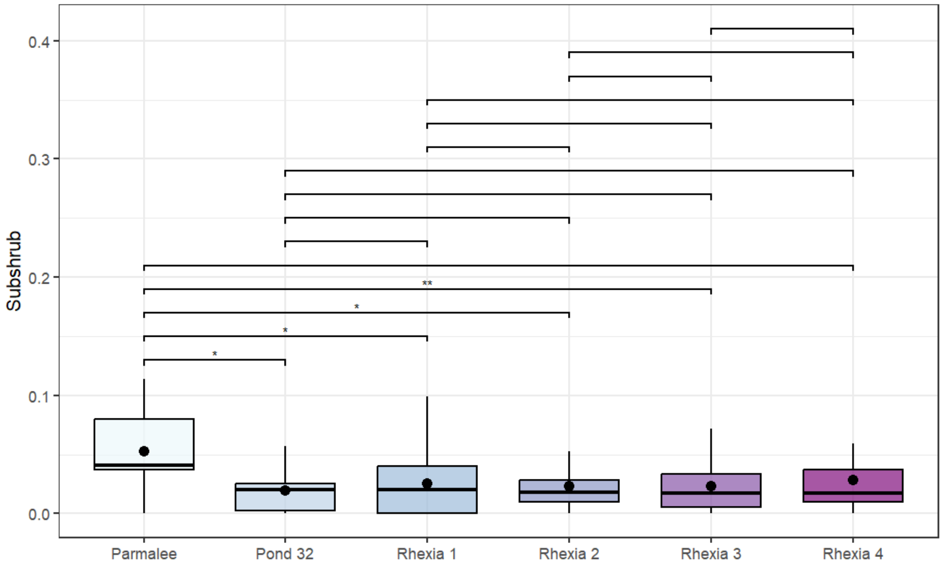
(d)


Legume
0.0
0.2
0.4
0.6
0.8
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4
*
***
*
***
**
****
*
****

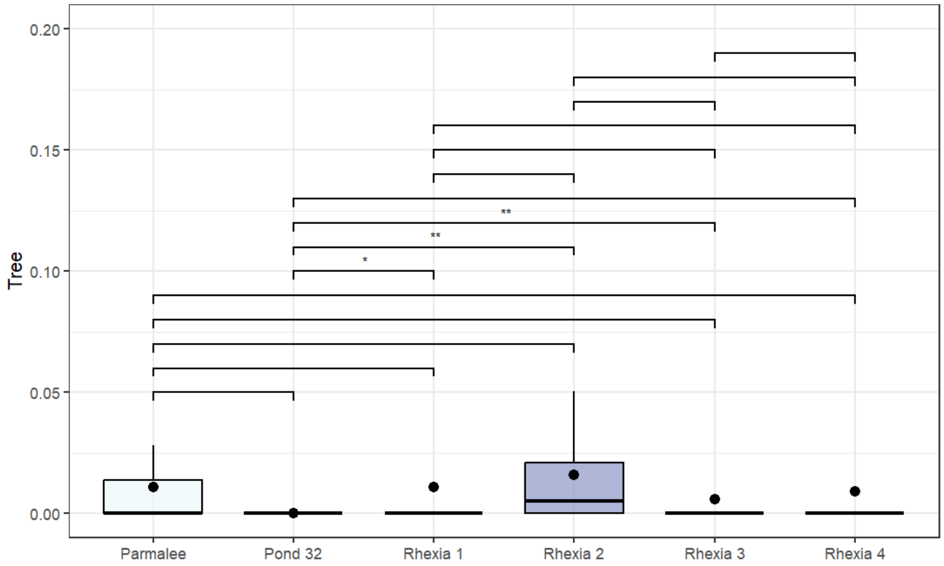
(e)


Shrub
0.0
0.2
0.4
0.6
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4
****
*
****
****
****
*
****
****
*
****
***

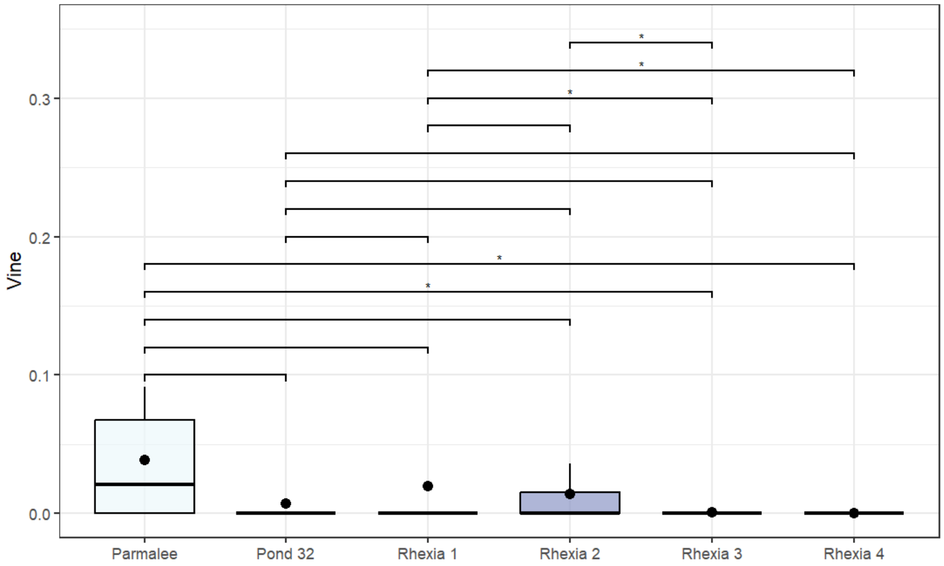
(f)


Subshrub
0.4
0.3
0.2
0.1
0.0
**
*
*
*
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

(g)


Tree
0.20
0.15
0.10
0.05
0.00
**
**
*
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

(h)

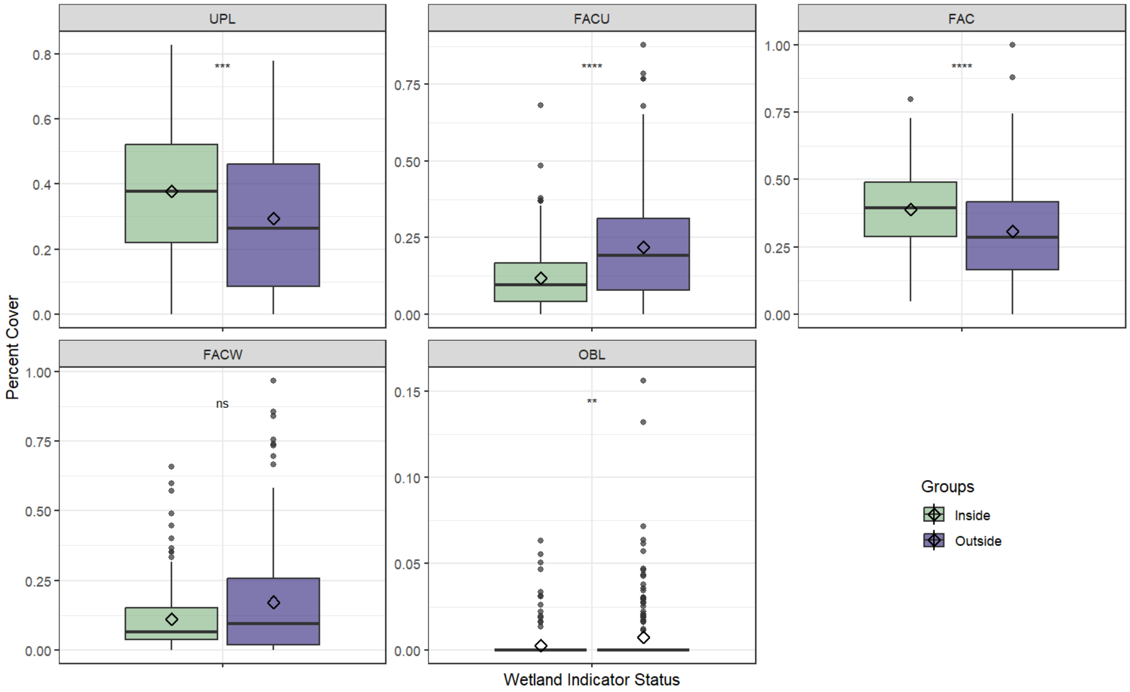


(i)

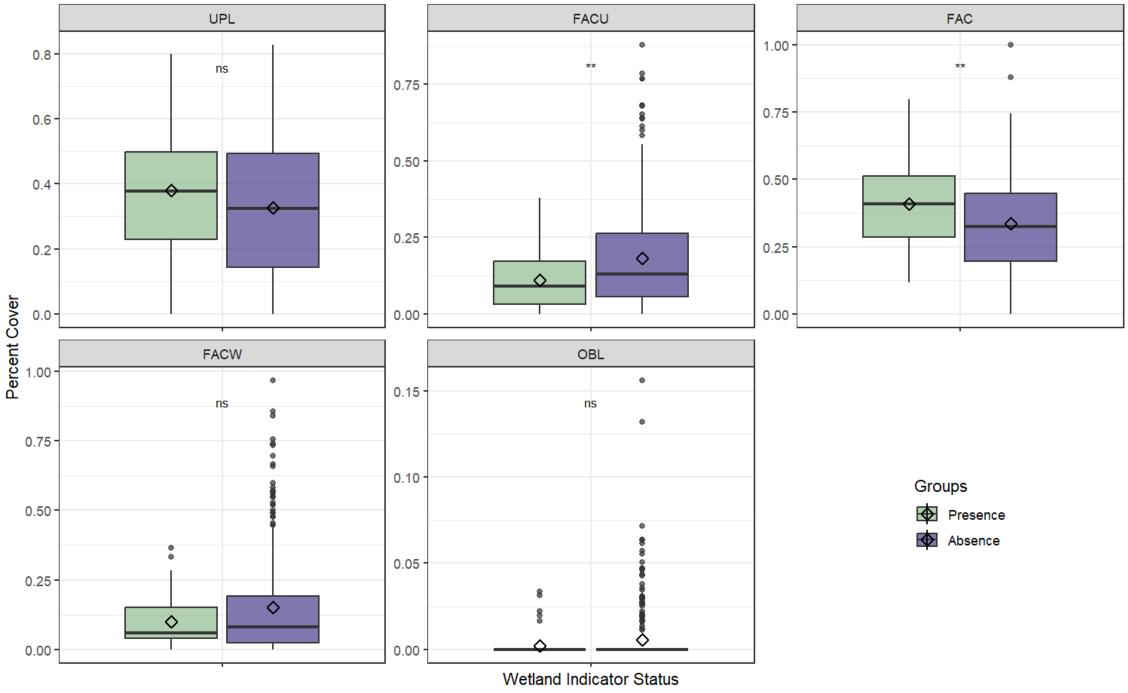
Figure 17. Mean cover of different growth forms compared across sites. Statistically significant differences are marked with * for differences at alpha = 0.05, ** for differences at alpha = 0.01, and *** for differences at alpha = 0.001.

There were also differences in Wetland Indicator Status (WIS) across categories. When comparing Inside and Outside groups, there were significant differences in Wetland Indicator Species cover across all WIS except Facultative Wetland (FACW) (Fig. 18a). There was more Upland (UPL), Z = 3.176, $p < 0.001$, and Facultative (FAC) cover, Z = 4.105, $p < 0.001$, in the Inside group. The Outside group had more Facultative Upland (FACU), Z = 4.69, $p < 0.001$, and Obligate Wetland (OBL), Z = 2.78, $p = 0.003$, cover than the Inside group.

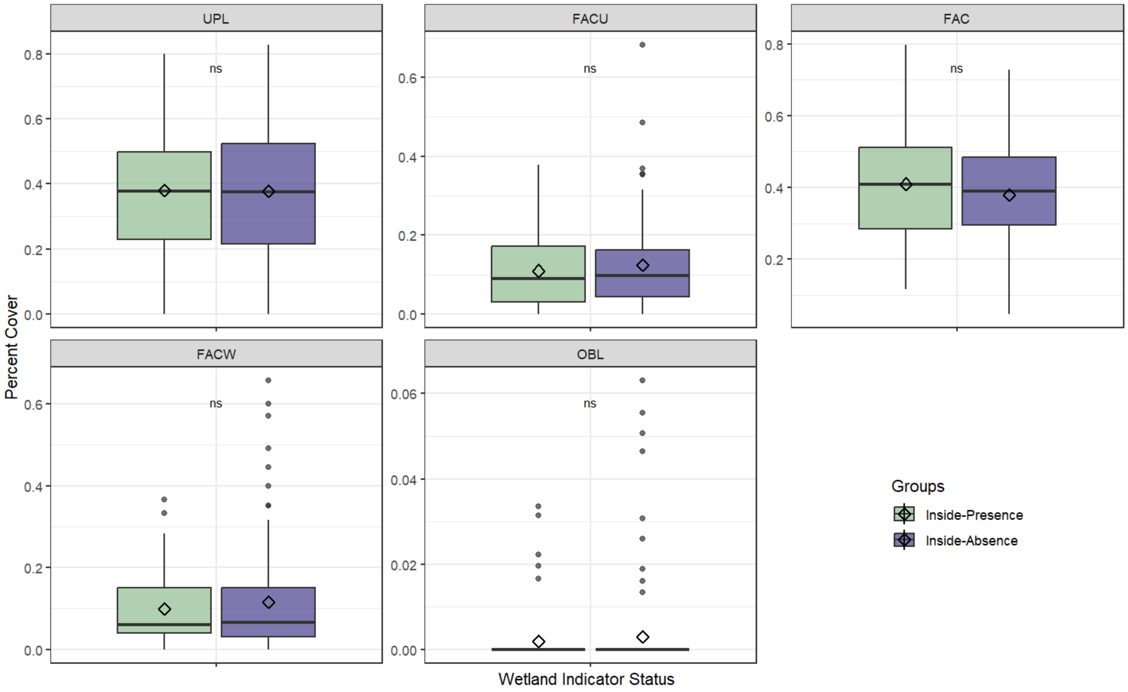
There were significant differences between Schwalbea Presence and Absence groups in WIS cover as well (Fig. 18b). The Presence group had significantly more FAC cover, Z = 3.073, $p = 0.001$ and marginally more UPL cover, Z = 1.526, $p = 0.064$ than the Absence group. There were no differences in WIS composition between Inside-Presence and Inside-Absence plots (Fig. 18c).


UPL
FACU
FAC
FACW
OBL
***
****
****
ns
**
Percent Cover
Wetland Indicator Status
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00
0.05
0.10
0.15
Groups
Inside
Outside

(a)


UPL
FACU
FAC
FACW
OBL
ns
**
**
ns
ns
Percent Cover
Wetland Indicator Status
0.0
0.2
0.4
0.6
0.8
0.00
0.25
0.50
0.75
1.00
0.05
0.10
0.15
Groups
Presence
Absence

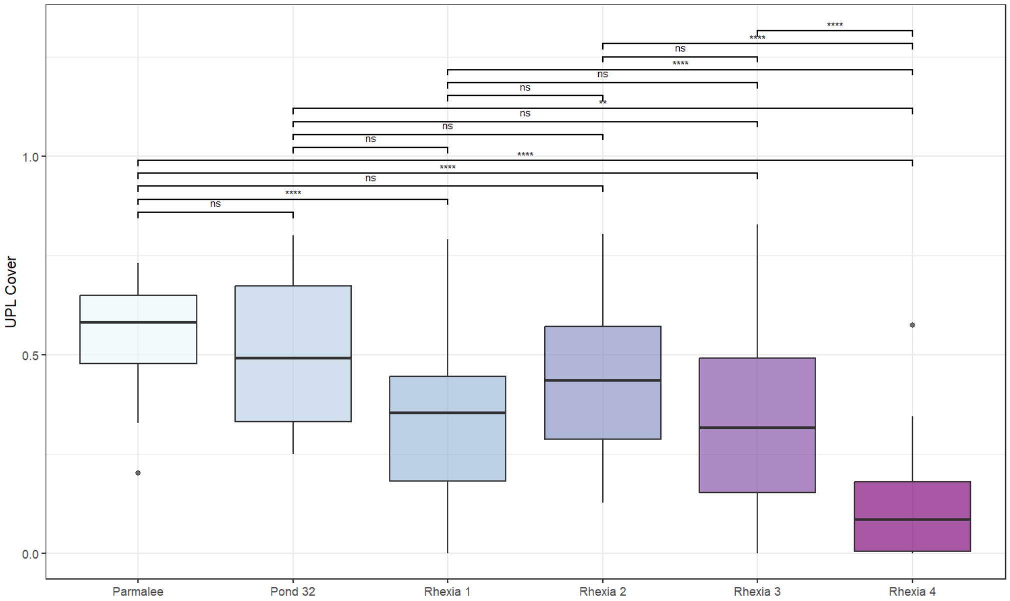
(b)



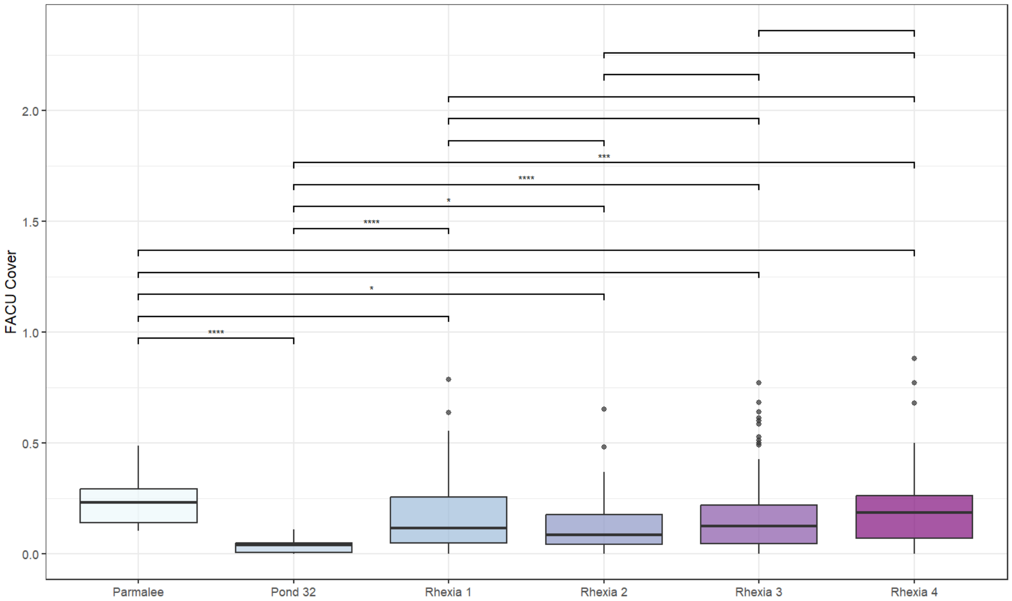
(c)

Figure 18. Differences in Wetland Indicator Status composition between groups. Groups are (a) Inside-Outside groups, (b) Presence-Absence groups, and (c) Inside-Presence and Inside-Absence groups.

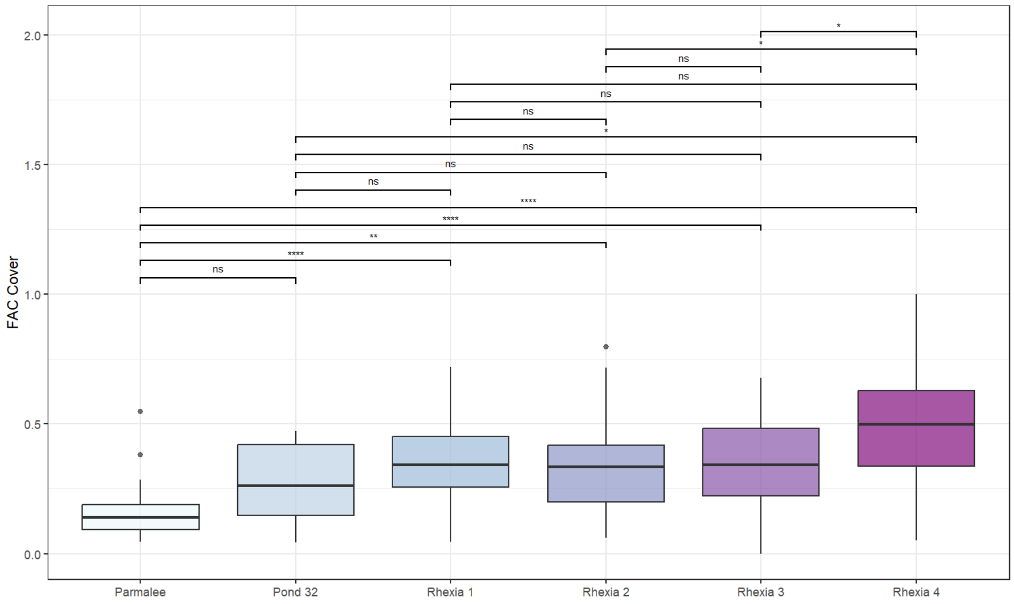
There were significant differences across sites in Wetland Indicator Status cover as well. Parmalee had more UPL cover than Rhexia 1, 3, or 4 (Fig. 19a). Pond 32 had more UPL cover than Rhexia 4. Rhexia 1, 2, and 3 had more UPL cover than Rhexia 4. Parmalee had more FACU cover than Rhexia 2, and Pond 32 had less FACU cover than every other site (Fig. 19b). Parmalee had less FAC cover than every other site except Pond 32 (Fig. 19c). Pond 32 and Rhexia 3 had less FAC cover than Rhexia 4. Parmalee had less FACW cover than every site except Pond 32 and Rhexia 2 (Fig. 19d). Rhexia 3 had more OBL cover than Pond 32, Rhexia 1, and Rhexia 2 (Fig. 19e).


****
****
ns
****
ns
ns
**
ns
ns
ns
****
****
ns
****
ns
1.0
0.5
0.0
UPL Cover
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

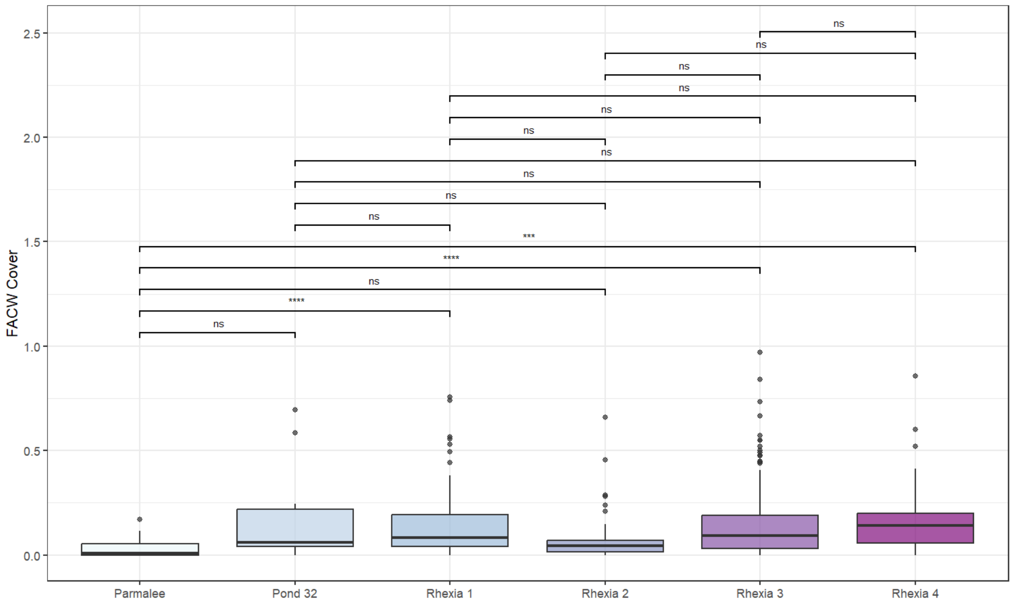
(a)


***
****
*
****
*
****
2.0
1.5
1.0
0.5
0.0
FACU Cover
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4

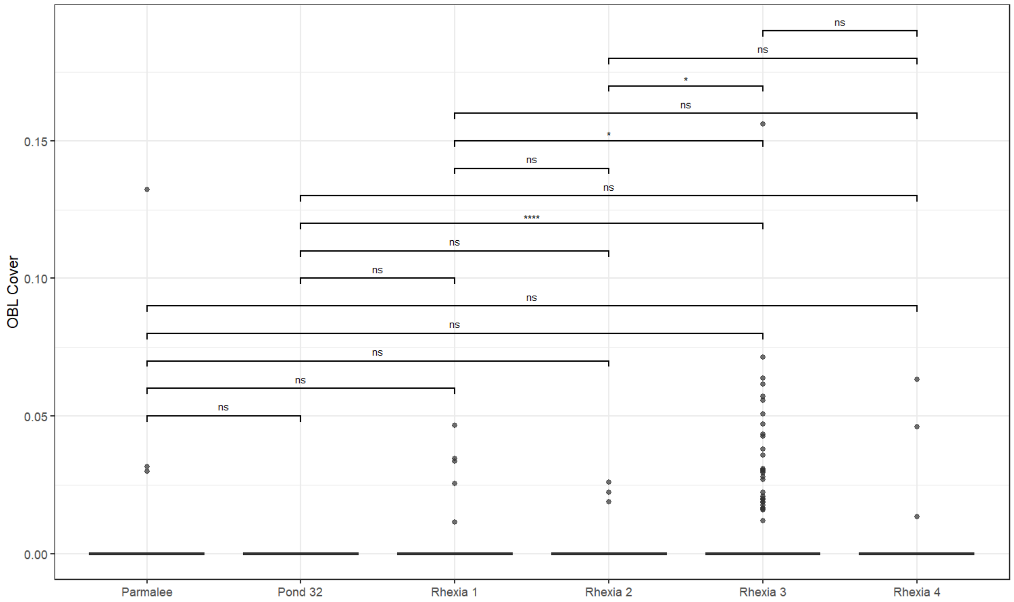
(b)


FAC Cover
2.0
1.5
1.0
0.5
0.0
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4
*
*
ns
ns
ns
ns
*
ns
ns
ns
****
****
**
****
ns

(c)


FACW Cover
2.5
2.0
1.5
1.0
0.5
0.0
Parmalee
Pond 32
Rhexia 1
Rhexia 2
Rhexia 3
Rhexia 4
ns
ns
ns
ns
ns
ns
ns
ns
ns
ns
***
****
ns
****
ns

(d)

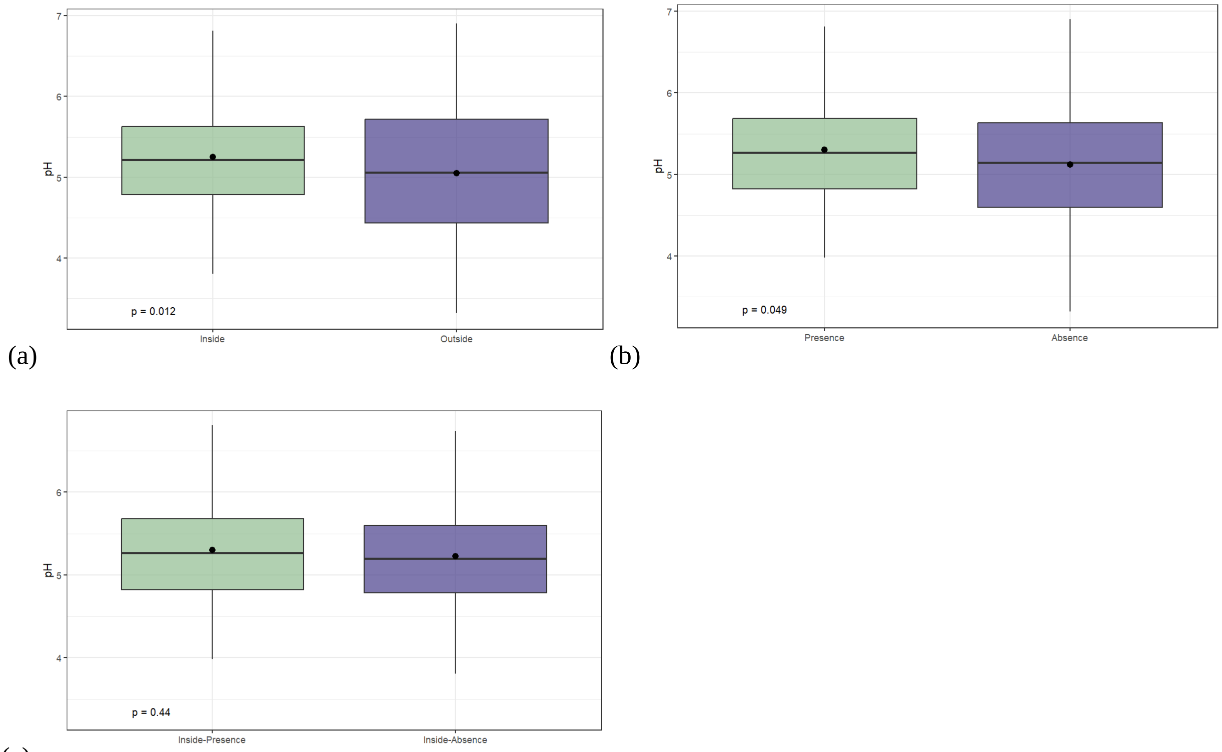


(e)

Figure 19. Differences in cover of the five Wetland Indicator Statuses across sites.

<u>pH</u>

There were significant differences in pH measurements. The Inside group had a significantly higher pH than Outside groups (Fig. 20a), t(310) = 2.52, *p* = 0.012, and the Presence group had a higher pH than the Absence group (Fig. 20b), t(108) = 1.99, *p* = 0.049. The Inside group had a mean pH of 5.25 while the Outside group had a mean of 5.05. The Presence group's mean pH was 5.30, and the Absence group's pH was 5.11. There were no differences between the Inside-Presence and Inside-Absence groups, t(126) = 0.77, *p* = 0.443 (Fig. 20c). There were differences in pH by Site (Fig. 21). Rhexia 1 had a higher pH than any site except for Pond 32. Parmalee, Pond 32, and Rhexia 2 had higher pH than Rhexia 3 and Rhexia 4. Rhexia 4 had lower pH than any site.



(a) (b)

(c)

Figure 20. Differences in mean pH between groups. Groups are (a) Inside-Outside groups, (b) Presence-Absence groups, and (c) Inside-Presence and Inside-Absence groups.

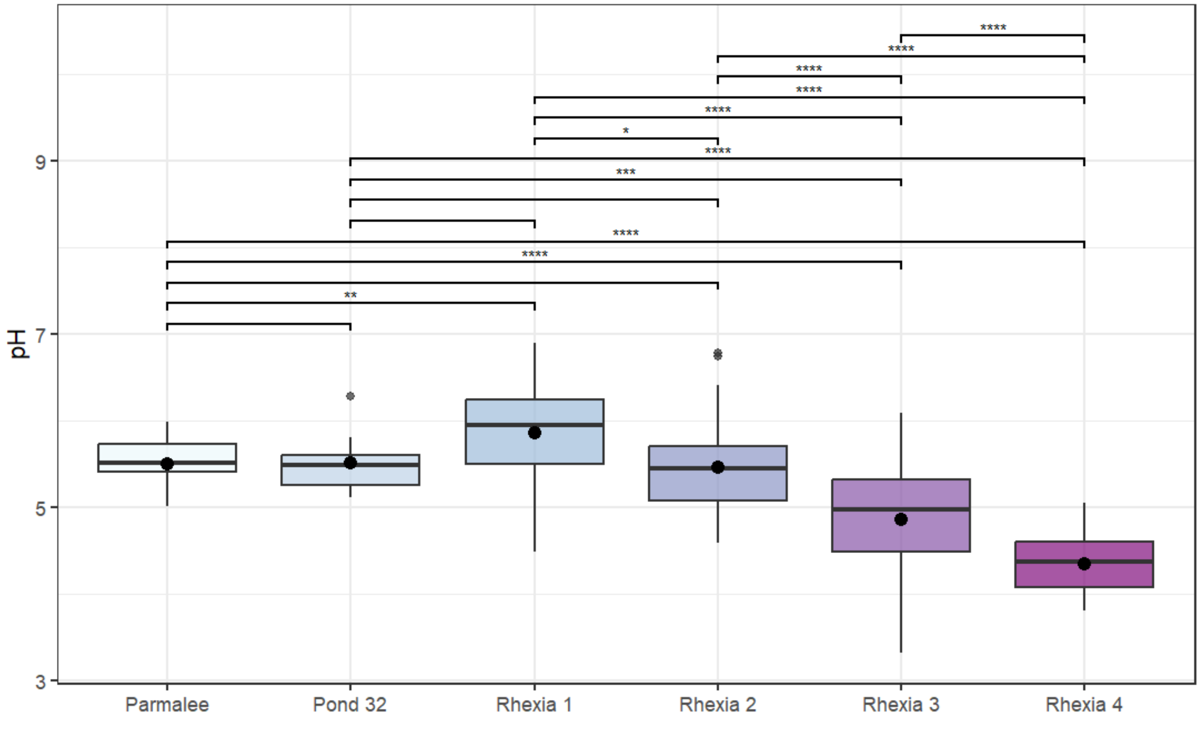


Figure 21. Differences in mean pH across Schwalbea sites at Ichauway.

3.4 Discussion

Indicator species

Indicator species analysis performed at different levels revealed overlap in indicator species between the Inside-Outside groups and Presence-Absence groups. Aside from *Dyschoriste oblongifola* (Michx) Kuntze and *Schizachyrium tenerum* Nees, all eleven species identified as indicative of the Presence group at the p = 0.01 level were also identified as indicators of the Inside group. *D. oblongifolia* and *S. tenerum* were identified as indicators at the p = 0.05 level for the Inside group. This indicates two things: (1) There are fine-scale differences in species composition where Schwalbea is visibly growing compared to where it is not, and (2) These differences translate to the broader scale of Inside or Outside the bounds of populations and subpopulations as well. If there had been substantial differences in indicator species between these groups, the results would be less transferable in the field due to microsite differences in species composition where Schwalbea is actually growing, even within the bounds of the population. The species found to indicate the Outside group did not transfer to the Absence group, most likely because the Schwalbea Absence group also included plots defined as Inside.

Two species indicative of the Inside group, *Hypericum suffruticosum* W.P. Adams & Robson and *Tragia smallii* Shinners, were found to be significant at the p = 0.05 level for the Presence group but not at the 0.01 level. One species found to be indicative of the Inside group was not indicative of the Presence group. This was *Xyris caroliniana* Walter, a facultative wetland species. Since Schwalbea is an ecotonal plant, and often grows alongside both upland and wetland species, it is helpful to identify possible limits of suitability on the uplant-wetland scale. It is possible that the conditions in which *X. caroliniana* grows are too wet for Schwalbea, and represent an outer edge of suitability for the species. *X. caroliniana* might mark the often-invisible gradient (due to summer dry periods, for instance) at which point environmental conditions are transitioning to wetland rather than ecotone. Because ecotones can vary widely in size and species composition, these types of botanical cues could be helpful in determining suitable habitat for outplantings or in providing visual cues while searching for Schwalbea in the field.

Kelly (2006) and Kelly & Denhof (2022) found nine species to be indicative of Schwalbea habitat in New Jersey. Three of these are found on Ichauway: *Chrysopsis mariana* (L.) Elliott, *Ionactis linariifolia* (L.) Greene, and *Schizachyrium scoparium* (Michx.) Nash./*Andropogon virginicus* L. These latter two grasses were combined into one species called *Schizachyrium scoparium* in Kelly's (2006) study because of difficult vegetative identification. In the present study, *C. mariana* was also found to be an indicator species of Schwalbea. *S. scoparium* was not identified in this study, and *Andropogon* species were lumped into a single separate species. However, another species in the genus *Schizachyrium*, *S. tenerum*, was found to be an indicator species for Schwalbea. This species is not found in New Jersey. The other six species found to be indicators in New Jersey are, in turn, not found on Ichauway: *Solidago nemoralis* Aiton, *Hieracium venosum* L., *Eurybia spectabilis* (Aiton) G.L. Nesom, *Liatris pilosa* (Aiton) Willd., *Polygala brevifolia* Nutt., and *Gaultheria procumbens* L. The first four of these are asters, the fifth is in the family Polygalaceae, and the sixth is in the family Ericaceae.

Of the species at Ichauway found to be indicators of Schwalbea, only three are found in New Jersey, and only two were recorded at the site Kelly (2006) studied. Of these two, *C. mariana* was also found to be an indicator species for Schwalbea. The other species found was *Pteridium pseudocaudatum* [formerly known as *P. aquilinum*] (L.) Kuhn. Although this species was neither positively nor negatively associated with the Schwalbea in New Jersey overall, it was strongly negatively associated with two specific subpopulations there, mirroring the trend observed at Ichauway.

The species found to be indicators of Schwalbea at Ichauway that are not found in New Jersey are three species in Asteraceae, three in Poaceae, and one each in Acanthaceae, Cistaceae, Euphorbiaceae, Hypericaceae, and Xyridaceae. Asters accounted for approximately 27% of the indicator species at Ichauway and 70% of the indicators in New Jersey, although they only accounted for 16% and 30%, respectively, of overall species richness. At Ichauway, the family Poaceae was also heavily represented in the indicator species identified (27%), but no species in Poaceae were found to be indicators in New Jersey. A higher diversity of families were identified as indicators in Georgia than New Jersey. This could be due simply to differences in overall species richness since there were 67 associate species identified in

New Jersey, and 218 associate species observed at Ichauway (Kelly, 2006). It could also be a result of management. The New Jersey population has not been historically managed with fire, while the Ichauway populations are burned every couple of years at least.

Identifying bioindicators of rare species habitat can be helpful for translating unmeasured or unknown environmental gradients into measurable phenomena. While it is known that Schwalbea grows in ecotones, not all ecotones are alike. Different wetlands support unique assemblages of plants, and their ecotones do as well. Knowing species that are indicative of Schwalbea habitat in portions of the southern range will allow conservation biologists to determine suitability of different ecotones more clearly for Schwalbea growth. Moreover, the species indicated here are common G5 and G4 species and should be easily found in other places. These bioindicators might not, however, translate to Schwalbea habitat beyond the measured extent of the range in Georgia.

Functional groups

Ecologists have long used plant functional traits as ways of describing and monitoring change in plant communities, and this non-taxonomic classification system continues to grow (Arnold, 1955; Boutin & Keddy, 1993). Functional groups have been used to assess and describe different types of wetlands (Flinn et al., 2008), to examine responses of communities to fire regime and other disturbances (Arnold, 1955; Gill & Burke, 1999; Peterson et al., 2007), and to monitor rare plant communities (Franks et al., 2009). Increasingly, attention is being given to how functional groups affect and are affected by belowground processes such as nutrient cycling and carbon storage as mediated by biotic soil communities (Laliberté, 2017) and the implications of this for monitoring community responses to climate change (Bargett, 2017; Gill & Burke, 1999).

While knowledge of very basic functional groups such as those measured here (growth form and wetland indicator status) do not convey the detailed information that other trait measures such as root structure, pollinator strategy, or specific leaf area could, this information could serve as a good baseline from which to monitor the community. Here, it was determined that there were about 2% more asters growing in Inside plots as opposed to Outside. There were about 4% more graminoids growing Inside than Outside Schwalbea populations. There were about 4% more shrubs growing Outside populations than Inside, and there were about 2% more vines growing Outside than Inside, where there were almost none growing. These differences in composition could reflect underlying soil conditions that would be difficult and costly to monitor without the aid of aboveground vegetation (Gill & Burke, 1999; Laliberté, 2017). Since Schwalbea is an ecotonal plant, it could be reliant on the fluctuating hydrological properties of ecotonal soils. Changes in functional group composition, such as increased shrub or vine cover near Schwalbea populations, could indicate changes in the hydrology itself that might not be obvious to the unaided eye (Brownstein et al., 2015). Thus, the relatively simple assessment of percent cover of various functional groups could aid in monitoring changing moisture conditions due to environmental and climate change, which are threats to many plants, but especially to endangered ones since they are already vulnerable.

The compositional differences in Presence and Absence groups aligned with the differences between Inside and Outside groups for the most part. Shrubs, vines, and graminoids followed the same trends, while differences in subshrubs and trees also became significant. There was approximately 1% more subshrub cover in Absence groups than Presence groups, and about 2% more tree cover. When examining Inside-Presence and Inside-Absence groups, Aster compositional differences were again statistically significant, but in the opposite direction. There was approximately 2% more Aster cover in the Absence group than the Presence group. Since the Inside group had more Aster cover than the Outside group, this could indicate Schwalbea’s preference for Asters as potential hosts, but also a need for some level of distance from them as well. In other words, preferable Schwalbea habitat should contain a higher concentration of Asters than the surrounding land as a whole, but on the microsite level, there should be less Asters than the immediate surroundings. This could be a result of asters being not only potential host plants but also potential competitors for resources. Another difference that became apparent only on the finer scale of interior Schwalbea habitat was that non-Aster forb cover was about 2% higher in places where Schwalbea grew versus where it did not. Legume cover was about 2% less in areas with Schwalbea versus without. These finer-scale distinctions could aid conservationists in selecting sites for outplanting or in determining locations for augmenting known populations.

Differences in wetland indicator groups were also revealed here. Somewhat intuitively, Outside groups had higher cover of FACW and OBL species, which would be expected since Schwalbea does not grow inside of wetlands but rather in the ecotones surrounding them. Outside groups also had more FACU cover, but less UPL and FAC cover. Inside Schwalbea populations probably exhibited more FAC species since ecotones represent the outer edges for both upland and wetland species, and those dwelling within ecotones are likely capable of adapting to both wet and dry conditions. It is unexpected, however, that Inside groups contained more upland species than the Outside group. It is possible that the Outside group was sampled more from the wetland and ecotone side than from the upland side of the Schwalbea populations. The Schwalbea Presence-Absence groups followed similar patterns. The Presence group also contained higher cover of FAC and lower levels of FACU and FACW than the Absence group. Because the Absence group contained plots from both the Inside and Outside groups, there was not more cover of OBL species, however. There was also not a significantly larger percentage of UPL species in the Absence or Presence group.

The information here, while indicating ecologically important differences in Schwalbea habitat, is questionable in its applicability. While there were significant differences in functional group composition, these were on a scale of 2-4% changes. However, sampling took place within two months after fire, during Schwalbea's flowering period. Differences in cover noted here might be amplified with longer time since fire. The small, but significant, variation observed here would be difficult to assess in the field without plot-based sampling. However, overall trends could aid land managers in determining whether site conditions are changing and becoming less suitable for Schwalbea. For instance, while vine cover was low overall, it was significantly lower in areas associated with Schwalbea (Inside and Presence groups). If vine cover was to begin encroaching into Schwalbea habitat, this could signal worsening habitat favorability. Since Schwalbea is declining across much of its range, early detection of vegetation changes that could affect this rare plant's persistence is important.

pH

The Inside and the Presence groups both had significantly higher pH values than the Outside or Absence groups overall. Given that the range of pH for the Inside group was 3.81 – 6.81, but the mean pH for soils in which Schwalbea was visibly growing was 5.30, there seems to be a preference for an intermediate pH. There are differences in mean pH across sites, however, and in some sites, Schwalbea is found growing in soils with higher pH than the surroundings, while in other sites, the reverse is true. The range of pH values for soils with Schwalbea is 3.98 – 6.81. This could indicate that there are not strict confines of pH values for this plant, but rather that pH limits Schwalbea in combination with some other factor(s). Interestingly, the site with the lowest overall pH (Rhexia 4) is also the site with the smallest Schwalbea numbers, excluding those affected by Hurricane Michael in 2018.

Kelly (2001) found similar trends in the pH measurements in New Jersey Schwalbea populations. Soils in which Schwalbea grew had higher pH than the soils downslope of Schwalbea. Schwalbea soils had a mean pH of 4.7 ± 0.2 while downslope soils had a mean pH of 3.7 ± 0.1. The differences between groups in New Jersey was more pronounced than the differences in the Ichauway populations. Measurements here also aggregate several populations, with a fairly large range in pH. Furthermore, this study did not distinguish between upslope and downslope Outside and Absence plots. Nonetheless, the differences found here did mirror the New Jersey results in that soils in Schwalbea plots had higher average pH than plots without Schwalbea (Absence plots) or plots from Outside Schwalbea populations. The observation that there are differences in pH between soils with and without Schwalbea and within and outside of populations confirms the importance of this variable for the species' ecology. Still, more must be learned about what combination of conditions allows for Schwalbea to tolerate lower or higher pH values at different sites.

Chapter 4: Modeling habitat suitability for *Schwalbea americana*

4.1 Introduction

It is well known that biodiversity is being lost at an alarming rate (Wake & Vredenberg, 2008; Pereira et al., 2010; Johnson et al., 2017; Wang & Gamon, 2019). One way the conservation community addresses this threat is by identifying and establishing Protected Areas and Key Biodiversity Areas, or KBA's (Prendergast et al., 1999; IUCN, 2016; Kullberg et al., 2019;) in order to preserve the ecosystems that harbor the most biodiversity. Another conservation strategy used since the 1960s is the classification of extinction risk (Mace et al., 2008). The International Union for the Conservation of Nature's (IUCN) Red List for classifying risk of extinction (IUCN, 2022) was one of the original tools of classification. It was created to guide conservation actions and objectively describe categories of extinction risk (Mace et al., 2008). Organizations classifying extinction risk in the United States are individual states, the federal government under the Endangered Species Act, and NatureServe (NatureServe, n.d.). To date, vertebrates have received highest priority in classification, but plants and fungi are beginning to receive more attention (Lughadha et al., 2020). One of the objectives of identifying a species as at risk of extinction is to increase conservation actions for such species. Modeling habitat suitability for rare and endangered species is increasingly used as a conservation action since it can guide establishment of new Protected Areas and help locate new populations (Loiselle et al., 2003; Guisan et al., 2006; Peterson, 2006; Rodriguez et al., 2007; Gogol-Prokurot, 2011; Guisan et al., 2013; Goncalves et al., 2016; Sofaer et al., 2019).

Maxent (Phillips et al., 2006) is an algorithm increasingly used in the modeling of both common and rare species (Bosso et al., 2013; Hohmann & Wall, 2016; Ma & Sun, 2018; Huercha et al., 2020; Ab Lah et al., 2021; Hale et al., 2021; Thakur et al., 2021). Like other habitat suitability models, Maxent combines known species occurrences with environmental variables to estimate habitat across a defined area (Phillips et al., 2004; Elith et al., 2011). However, unlike many other modeling techniques, Maxent does not require true absences. It can create robust models with pseudo-absences instead, which are points randomly selected from the defined region to represent those areas that are unsuitable for the species

(Elith et al., 2011). It is especially competent at rare species modeling because it can perform well with few occurrences.

Schwalbea americana is a federally endangered hemiparasitic plant native to the Coastal Plain in the eastern United States with a NatureServe ranking of G2 (globally imperiled). With less than twenty self-sustaining populations left on the planet, it is an excellent candidate for habitat suitability modeling (USFWS, 2018). This chapter describes the construction and evaluation of a Habitat Suitability Model built with Maxent for Schwalbea.

4.2 Methods

Element Occurrences

Element occurrence (EO) data for Schwalbea was obtained through Atlanta Botanical Garden's membership in the NatureServe Network (NatureServe, 2022) and through Florida Natural Areas Inventory (FNAI, 2022). EOs from Florida, Georgia, Alabama, South Carolina, and North Carolina were used in this model. Data for Louisiana was not available, and the Mississippi population has not been seen since 1902. One hundred and thirty-one occurrence points from the five states included are available. However, these data are uncleaned and include multiple individuals within the same populations as well as extirpated populations. Data were cleaned by consulting the EO notes for information about population viability, with extirpated populations being eliminated. Many of the remaining populations had not been visited in many years. Because it was not possible to visit every EO to ensure its continued existence, the coordinates for each were viewed in Google Earth to remotely assess current habitat. Those coordinates that occurred on visibly developed land were removed. After this process, 101 EOs remained.

These remaining 101 occurrences were further reduced to account for sampling bias and to remove replicated points (i.e., individuals) of the same population. An inherent assumption of habitat suitability models is that the entire area of interest has been sampled (Phillips et al., 2009; Kramer-Shadt, 2013; Yackulic et al., 2013). This is not usually the case since particular areas are more heavily sampled than others due to accessibility or assumptions about the habitat. Spatially thinning EOs is a recommended method of reducing sampling bias in the data to reduce overfitting (Kramer-Shadt, 2013;

Radosavljevic & Anderson, 2014; Kiedrzyński et al., 2017;). Overfitting results in higher scores for the model, but also in a less accurate model. Spatial thinning of the data has been found to reduce both omission and commission errors (Kramer-Shadt, 2013). Thus, the R program spThin (Aiello-Lammens et al., 2015) was used to thin the cleaned EOs. SpThin allows the user to set a thinning distance, but the default is 5 km. This means that any EOs within 5 km of each other will be iteratively thinned at random to leave only one point within 5 km. Iterations ensure that the highest number of occurrence points are preserved. Since Schwalbea is a rare species, a less conservative distance was selected, and the EOs were thinned to 3 km. This left 52 EOs for the final analysis. The exact coordinates are being kept confidential due to the endangered status of Schwalbea.

Predictor Variables

Initially, 26 environmental variables in raster form were considered for inclusion in the model. Soil layers at 30-meter resolution were obtained from the U.S. Department of Agriculture's SSURGO (2022) database and included layers pertaining to soil moisture: Depth to Water Table (April to June Minimum), Soil Drainage Class, and Available Water Storage (0-25 cm). An elevation layer at 10-meter resolution was obtained from the U.S. Geological Survey's Digital Elevation Model products (2022). Three vegetation cover layers at 30-meter resolution were obtained from Landfire (a-c, 2020). A Fuel Vegetation Cover layer represents fuel load across differing fire regimens. Existing Vegetation Cover represents percent canopy cover by life form. Biophysical Setting documents the vegetation type and fire regime that was likely present prior to European colonization. Tree Canopy Cover at 30-m resolution was obtained from the U.S. Fish and Wildlife Service (2016). A proximity to water layer was developed in ArcGIS Pro 2.9.0 (Esri 2022) utilizing the National Wetland Inventory Data (U.S. Fish and Wildlife Service, 2022). WorldClim's 19 bioclimatic layers at 1 km^2 resolution (Fick & Hijmans, 2017) were obtained from the WorldClim website accessed at https://www.worldclim.org/data/ worldclim21.html.

ArcGIS Pro 2.9.0 was used to prepare environmental rasters for inclusion in the model. Each raster was resampled to the same resolution and projected to North America Albers Equal Area Conic. Computational power restricted the ability to use a fine pixel size of 10-m across the entire five-state range. A coarser 1 km^2 resolution necessary in this case. After projecting and resampling, the rasters were clipped to match the defined study region. The study area was delineated by buffering the extent of Schwalbea EOs by 50 km into the Coastal Plain ecoregion. This was done to limit model over-fitting since increasing buffer size artificially increases model performance (Phillips, 2008; Merow et al., 2013). By creating a 50 km buffer, the pseudoabsences selected by the MaxEnt model are chosen from within the realm of possibility of Schwalbea occurring rather than from areas Schwalbea would not be at all likely to occur, which is not of interest.

To determine which environmental variables to include in the final analysis, a preliminary model was run in MaxEnt. Default settings were used, and the “Do Jackknife to Measure Variable Importance” option was selected. This allows the user to determine which variables contribute most to the model (Merow et al., 2014). Subsequently, variable correlation was examined in R by evaluating Pearson’s correlation coefficients. Although machine-learning lessens the problem (Elith et al., 2011), highly correlated variables make interpretation of results difficult (Heikkinen & Luoto, 2006), so those variables with Pearson’s correlation coefficients with an absolute value > 0.75 were removed. Only those variables that contributed more than 1% to the model were retained.

Maxent Model: Setting Parameters

Maxent Java version 3.4.4 was used to create the habitat suitability model for Schwalbea. Although default features are set, Maxent allows the user to define modeling parameters, and this is recommended (Merow et al., 2013; Radosavljevic & Anderson, 2014; Merow et al., 2014). One parameter that is adjustable is the regularization multiplier, which penalizes complexity in a model (Merow et al., 2013). Although set at a default of 1, increasing the regularization multiplier can help reduce overfitting (Phillips et al., 2004; Merow et al., 2013; Merow et al., 2014). To determine the best regularization multiplier for this model, practice models were run with regularization multipliers ranging from 0.5 – 5.

Because of fast Maxent Java run-time, it is possible to easily run models many times to determine optimal model functioning, evaluated by model AUC scores. AUC, or Area under the (Receiving Operator) Curve, is a common statistical measure of model fit (Elith et al., 2006). It signifies whether the model can differentiate between sites with and without the focal species. AUC scores over 0.70 are typically understood to indicate a useful model (Swets, 1988). Strong models that are not overfit will minimize the difference between test and training AUC values, which indicate model strength on test (withheld occurrences) and training (included) data (Hohmann & Wall, 2016). The number of test and training EOs are set by the user by choosing a random test percentage.

Another parameter that can be user-defined is the combination of features used. Features are ways of transforming, or making functions of, the environmental variables to build a model that best takes into account how those variables influence species distributions (Elith et al., 2011). They include linear, quadratic, product, hinge, and threshold functions (Valavi et al., 2022).

Model Testing: Site Visits

Maxent models produce a rasterized map that, for each pixel, contains a number from 0-1 representing probability of habitat suitability, with 1 being the highest probability and 0 the lowest. Once this was obtained, pixels were reclassified into four bins for visualization: (1) 0.0 – 0.5: *Lowest Suitability*, (2) 0.5 – 0.8: *Medium Suitability*, (3) 0.8 – 0.9: *High Suitability*, and (4) 0.9 – 1: *Highest Suitability*. For determining search sites, the High and Highest bins were combined.

Between late September and early November 2022, sites from each bin were visited in North Carolina, South Carolina, Georgia, Alabama, and Florida. These sites were selected from public Protected Areas to facilitate timely searches since public lands are easily accessible. Public lands were identified by overlaying the model's rasterized map output with a map of protected lands in the United States (USGS Gap Analysis Project, 2022). Twenty-nine Highest Suitability sites were visited. Eleven Medium Suitability sites were visited. Sixteen Lowest Suitability sites were visited. Half of the sites searched were ranked Highest Suitability to prioritize seeking new populations while testing the model. Finding new populations is an urgent goal included in the most recent Five-Year Review for the species (USFWS, 2018). Twelve of the visited sites were known populations, eight of which were ranked Highest Suitability, three of which were ranked Medium Suitability, and one of which was ranked Lowest Suitability. These sites were visited to compare habitat amongst populations.

Habitat data was collected at each visited site. Because the pixel size was rather large (1 km^2), the site was first surveyed to locate the most likely Schwalbea habitat. In particular, wetland ecotones were sought. If no ecotone was found, the next most likely area was identified. At these places, species data were recorded (Appendix Table A7). Up to ten dominant overstory and midstory and up to fourteen dominant herb layer species were recorded. If a site contained a dominant tree species, but that tree species only occupied space within the herb layer, that tree was recorded as an herb. The same species could be recorded as a dominant herb, midstory, and overstory species. The distinction was marked by adding an “H”, “O”, or “M" at the end of each species code. This additional information could be helpful in understanding the suitability of a site, since Schwalbea might grow with a species as a dominant “herb” but not as a dominant midstory or overstory tree. A densiometer reading was taken at the center of the ecotone, or most suitable place, at each site. General notes on the condition of the site were also documented.

Species data was formatted into presence-absence data in Excel and R for use in PC-ORD 7.10. A Nonmetric Multidimensional Scaling (NMS) ordination was conducted to analyze multivariate patterns in the community data among Highest, Medium, and Lowest Suitability sites to address whether the categories were ranked appropriately by the model. NMS is considered a strong statistical tool for use in “messy” species datasets, when assumptions of normality cannot be met and there is a large percentage of zeros (McCune & Grace, 2002; Dexter et al., 2018). NMS organizes the dataset into a reduced dimensionality for easier interpretation of patterns. It reduces the stress, or distortion, required to fit entities originally placed on axes with high dimensionality onto a minimum number of axes while preserving rank-order among them (Kruskal, 1964; Clarke, 1993; Dexter et al., 2018). For this NMS procedure, a Sorensen distance measure was used. Ties in the dissimilarity matrix used to produce the ordination were handled with Kruskal’s secondary approach, which penalizes unequal ordination distances and thus results in higher levels of stress in the ordination (Dexter et al., 2018). Ties are more likely to occur in presence-absence datasets like the one used here (McCune & Grace, 2002). Random points were used for the starting configurations. Five thousand runs with real data were performed. Final dimensionality was determined by two criteria (Multivariate Analysis Course, Peck, 2022): (1) By adding an additional dimension, was stress reduced by at least eight points? (2) Does each additional axis explain at least 10% of the variance in the data?

4.3 Results

The final Habitat Suitability Model utilized five bioclimatic variables and two environmental variables. These variables and their contributions to the model are listed in Table 7. Jackknife of regularized training and test gain for variable importance are depicted in Figure 22. Forty-five presence records were used for training, and seven (15%) were used for testing. A regularization multiplier of 3.5 was found to be best for this model. Hinge, product, linear, and quadratic features were used. This model performed well as determined by AUC, with a training AUC = 0.988 and test AUC = 0.924 (see Figure 23). The rasterized map output of the model is shown in Figure 24.

Table 7. Variable importance for habitat suitability model. Percent contribution refers to the increase in regularized training gain attributed to that variable. Permutation importance is calculated by randomly permuting each variable on training and background data and assessing the effect of this on model training AUC scores. The score is normalized as a percentage.

Variable	**Percent Contribution**	**Permutation Importance**
Biophysical Setting	49.7	19.4
Soil	23.7	65.5
Mean Temperature of Wettest Quarter (Bio 8)	11	7.3
Precipitation of Wettest Month (Bio 13)	6.9	1.8
Mean Diurnal Range (Mean of monthly (max temp - min temp)) (Bio 2)	3.6	2.4
Precipitation of Driest Quarter (Bio 17)	3.4	0.9
Precipitation of Warmest Quarter (Bio 18)	1.8	2.7

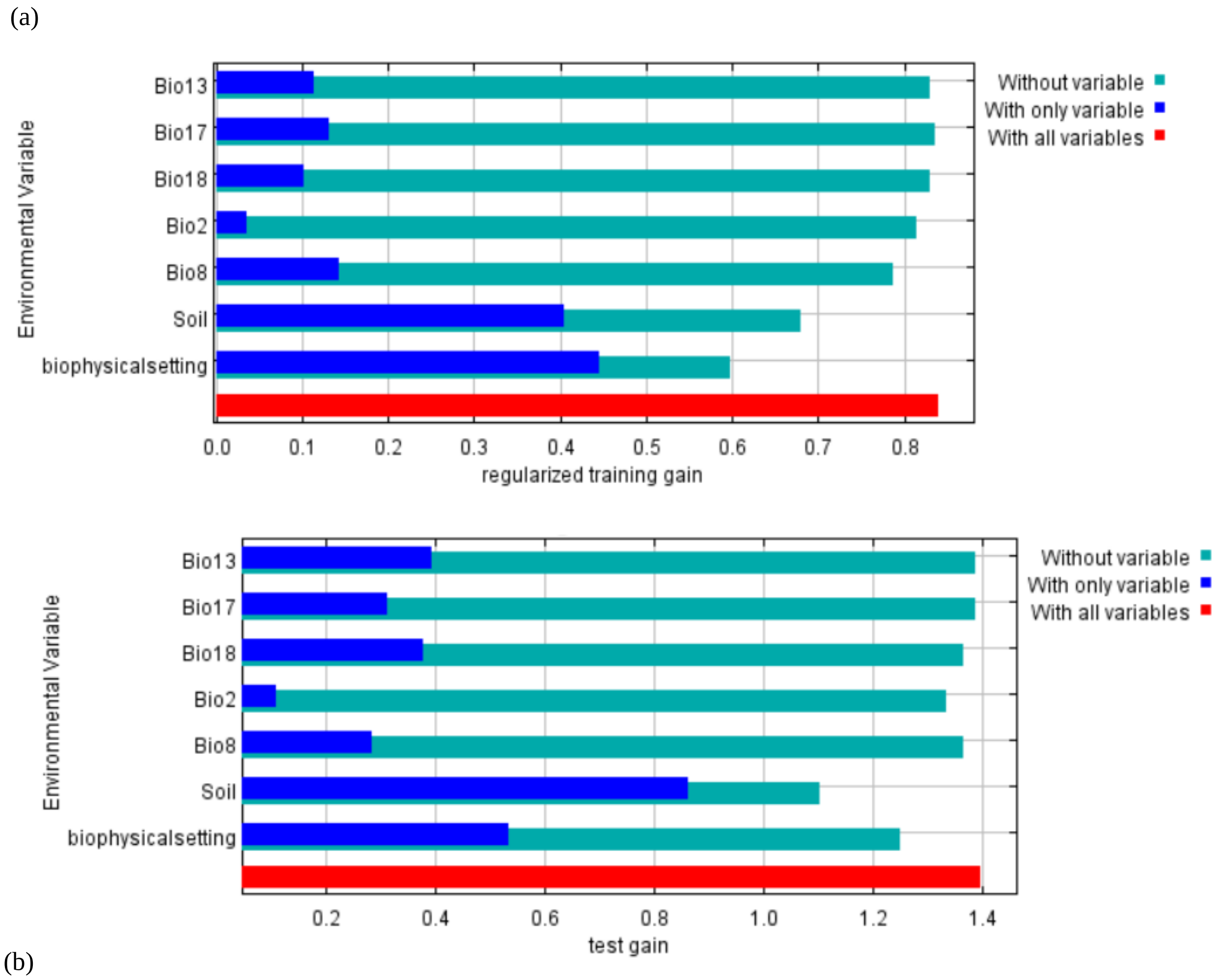


Figure 22. Jackknife of regularized (a) training and (b) test gain for variable importance in modeling habitat for **Schwalbea americana**. Training gain refers to the gains contributed to the model by each variable when using training data only. Test gain refers to the gains contributed to the model by each variable when testing it on withheld datapoints. The environmental variable with highest gain when used in isolation is Biophysical setting for training gain and Soil for test gain. These variables seem to have the most useful information by themselves. These two variables decrease the gain the most when they are omitted as well, indicating that they contain the most information that isn't present in the other variables.

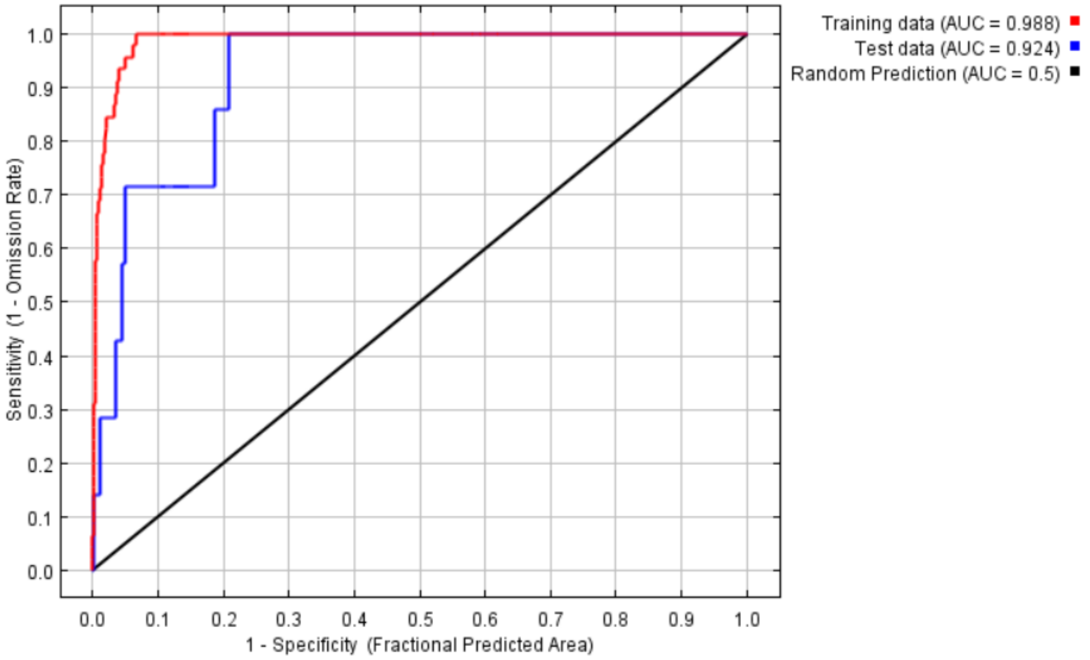


***Figure 23. Area under the receiver operating curve (AUC) for* Schwalbea americana *habitat suitability model*.** The curve depicts Sensitivity versus 1 – Specificity for this model.

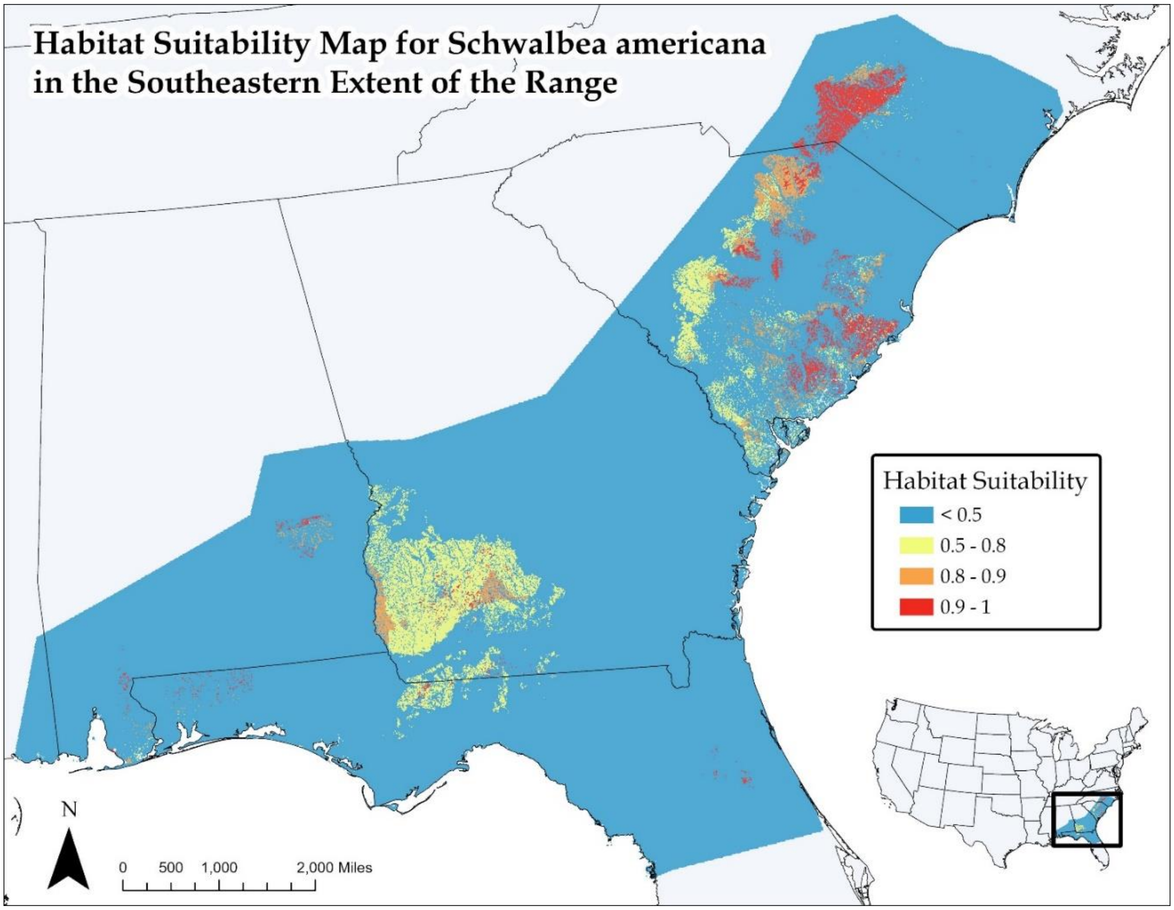
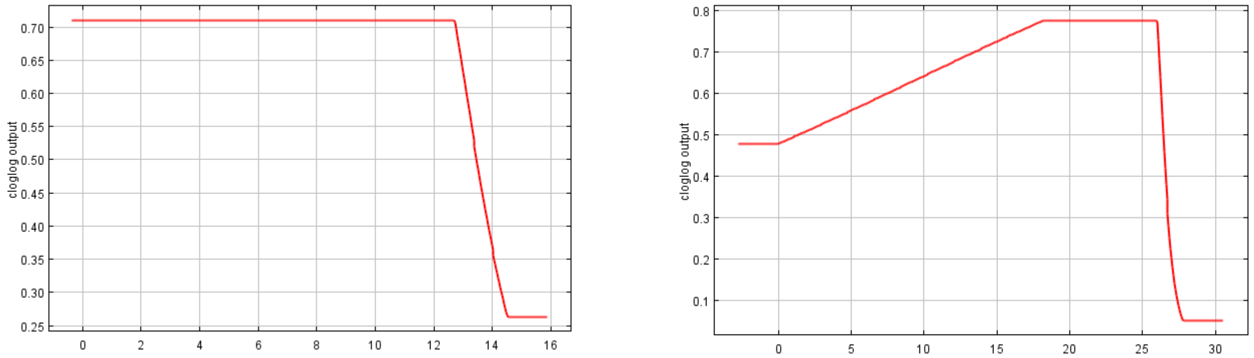


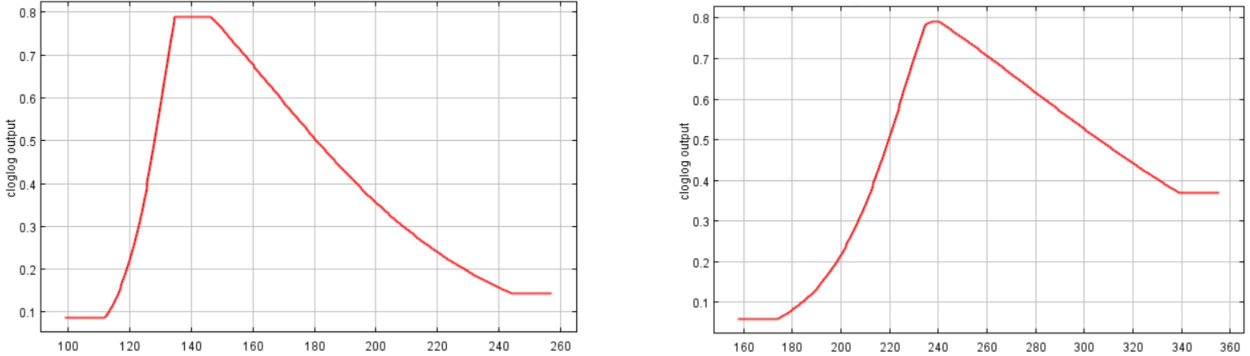
***Figure 24. Map of habitat suitability for* Schwalbea americana.**

Response curves produced in Maxent illustrate the preferred environmental conditions for Schwalbea. Schwalbea can tolerate a mean diurnal temperature range of 0-13° C. If the mean diurnal range exceeds 13° C, suitability declines sharply to nearly zero (Fig. 25a). Suitability increases as temperature increases from 0-18° C during the wettest quarter, and declines sharply past 26° C (Fig. 25b). In places where precipitation is below 110 mm during the wettest month of the year, Schwalbea is highly unlikely to occur (Fig. 25c). Schwalbea seems to prefer a range of 130-150 mm during the wettest month, beyond which suitability also declines. If the driest quarter of the year receives less than 170 mm of precipitation, there is very low chance of suitability, but at levels above 240 mm, suitability declines (Fig. 25d). If precipitation during the warmest quarter is below 300 mm, there is little chance that location is suitable for Schwalbea, but if precipitation is above 370, suitability declines (Fig. 25e). For Biophysical Setting, values correspond to physioecological historical setting. Habitat suitability centers most strongly around the 1450 values, which include Atlantic Coastal Plain Upland Longleaf Pine Woodland and Central Atlantic Coastal Plain Wet Longleaf Pine Savanna and Flatwoods (Fig. 25f). The 1290 group of values includes Southern Coastal Plain Dry Upland Hardwood Forest and Atlantic Coastal Plain Fall-line Sandhills Longleaf Pine Woodland among others. The 1770 values include East Gulf Coastal Plain Interior Upland Longleaf Pine Woodland and Southern Coastal Plain Mesic Slope Forest. Soil values correspond with particular soil types. For instance, 1380294 is the code for Albany Sands with 0-5% slopes and somewhat poorly drained soils, with a shallowest depth to water table of 53 cm. The suitable values indicate, overall, an ability to tolerate well-draining to poorly drained soils, but soils without much flooding capacity (Fig. 25g).



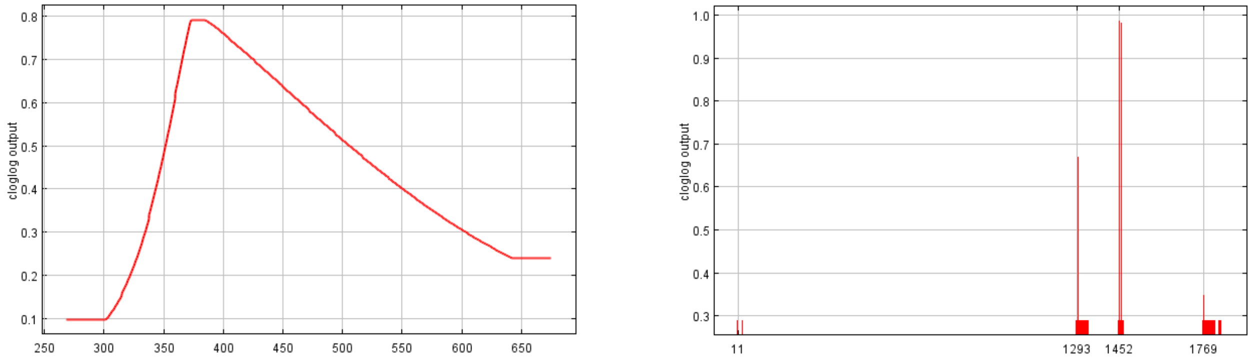
(a) Bio 2: Mean Diurnal Range (Mean Monthly [Max Temp – Min Temp])

(b) Bio 8: Mean Temperature of the Wettest Quarter



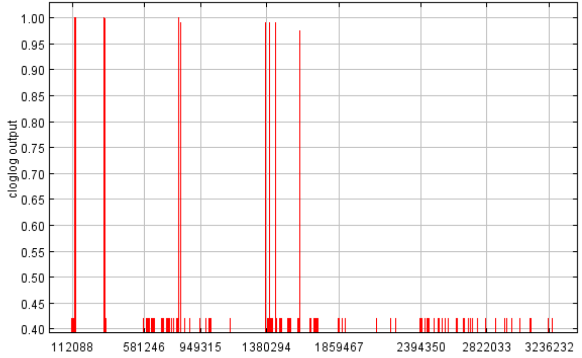
(c) Bio 13: Precipitation of the Wettest Month

(d) Bio 17: Precipitation of the Driest Quarter



(e) Bio 18: Precipitation of the Warmest Quarter

(f) Biophysical Setting



(g) Soil

Figure 25. Variable response curves (Maxent-produced). These plots show the relationship of predicted Schwalbea suitability with each environmental variable, with measurements of each variable on the X-axis and suitability from lowest (0) to highest (1) on the Y-axis.

Schwalbea americana was not found at any of the sites aside from sites with known populations. No Schwalbea was located at three of the known sites. Those sites (Doerun, Florida Bog site at Blackwater River State Forest, and Coldwater Horse at Blackwater River) had not been burned in 2022. Shrubs had grown relatively dense and *Aristida beyrichiana*, which only flowers with fire, was not flowering. Nine of the twenty-nine high suitability sites were noted as disturbed. Disturbance was marked either by logging, invasive species growth, possible feral hog ruts, or not enough fire. High suitability sites with altered fire regimes often contained plants which were commonly found near *Schwalbea americana* at known sites but which were overgrown if shrubs or trees (such as *Ilex glabra* or *Morella cerifera*), or crowded out by shrubs if herbaceous (such as *Rhexia mariana* or *Aristida beyrichiana*). *Aristida beyrichiana* found at fire-suppressed sites was not flowering. Logged sites either had been recently clearcut or had tire tracks and paths running through the area. Low suitability sites tended to be dominated by swamp or dense deciduous woods. However, one known and visited population (Quailridge site) was also classified by the model as lowest suitability. Three known visited populations were classified as Medium suitability (Doerun, Pond 32, and Rhexia).

NMS (Fig. 26) resulted in an ordination with two axes and a final stress score of 23.948. Adding a third dimension did not significantly reduce stress. The final ordination outperformed randomized data with a Monte Carlo test, $p = 0.004$. Final instability was 0.0065, and $R^2 = 0.9427$. Axis 1 could be explained on a forest-type level. The right side of Axis 1 is comprised mostly of plants like *Gaylussacia dumosa, Pinus palustris, Pteridium pseudocaudatum,* and *Aristida beyrichiana.* that are typical of intact open pine flatwoods and savannas (Weakley, 2020). The left side of the Axis is composed of species such as *Acer rubrum, Ilex opaca, Liquidambar styraciflua, Liriodendron tulipifera, Persea palustris,* and *Mitchella repens* that are more characteristic of deciduous forests, bottomlands, swamps, and/or disturbed areas. Axis 2 is composed of a continuum of species defined, at least in part, by preference for moist or dry conditions. Species such as *Agalinis fasciculata, Rubus cuneifolius, Trichostema dichotomum,* and *Callicarpa amerciana* which can tolerate drier, more disturbed conditions concentrate in the lower portion of Axis 2. The upper portion of Axis 2 is dominated by species that prefer wetter soils, such as *Clethra* *alnifolia*, *Persea palustris*, and *Ilex glabra.* See Table 8 for a full list of species strongly associated with each axis. Approximately 43% of variance was explained by Axis 1, and 26% by Axis 2.

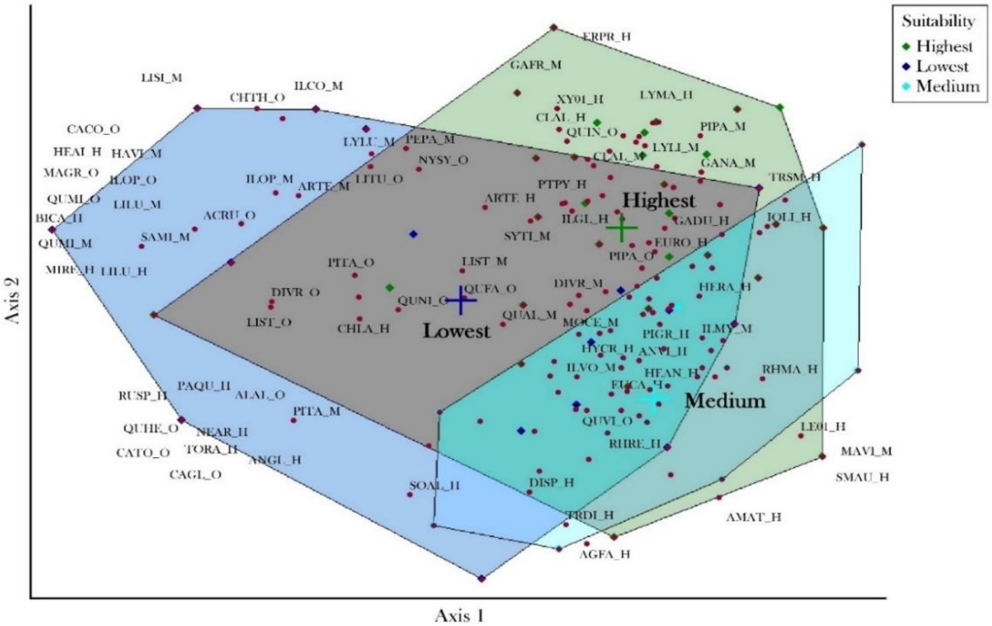


Figure 26. NMS ordination space for habitat suitability. Suitability refers to the suitability score for each visited site as determined by its modeled pixel value. Highest sites have suitability scores > 0.8. Medium sites have suitability scores between 0.5 and 0.8. Lowest sites have suitability scores < 0.5. Points reflect species in ordination space, represented by a four letter species code followed by a growth form marker. O refers to species which were dominantly Overstory at a site. M refers to species dominantly occupying the Midstory. H refers to herbaceous species, or woody species occupying a ground-level position in the habitat.

Table 8. Species associations with NMS axes for habitat suitability site visits. Species shown have correlation scores ≥ 0.5, thus strongly shaping the ordination space along these axes.

Species	**Axis**	**Direction**
*Andropogon spp.**	1	+
Aristida beyrichiana	1	+
Gaylussacia dumosa	1	+
Pinus palustris	1	+
Pteridium pseudocaudatum	1	+
Vaccinium myrsinites	1	+
Acer rubrum (overstory and midstory)	1	-
Ilex opaca (overstory and midstory)	1	-
Liquidambar styraciflua (overstory and midstory)	1	-
Mitchella repens	1	-
Persea palustris (midstory)	1	-
Pinus taeda (overstory)	1	-
Quercus nigra (overstory)	1	-

Liriodendron tulipifera (overstory)	1	-
Sabal minor (midstory)	1	-
Clethra alnifolia	2	+
Persea palustris	2	+
Ilex glabra	2	+
Tephrosia virginiana	2	+
Pinus palustris (overstory)	2	+
Rubus cuneifolius	2	-
Agalinis fasciculata	2	-
Quercus virginiana (midstory)	2	-
Solidago altissima	2	-
Pinus elliottii (overstory)	2	-
Callicarpa americana (midstory)	2	-
Trichostema dichotomum	2	-

**Andropogon* species were lumped into one category because of difficulty in distinguishing them vegetatively.

When overlaying the ordination space with the state in which each site is situated rather than each site's suitability, a clear pattern emerged (Fig. 27). Florida and Georgia overlap closely and are separate in ordination space from South Carolina and most of North Carolina, which overlap each other. There is some overlap between Georgia and North Carolina, and the only Alabama site is situated within Georgia's polygon.

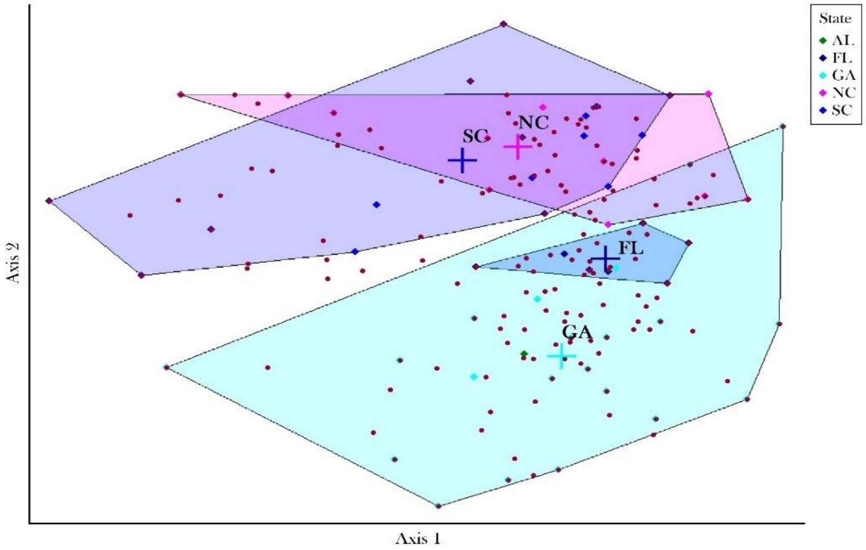


Figure 27. NMS ordination space: State overlay. Polygons encompass sites within individual states. Alabama is not displayed with a centroid or polygon because only one site in that state was visited (the diamond just left of the Georgia centroid's left line).

There were differences in the occurrence of some observed dominant species based on Suitability classification of the site. *Pinus palustris* as an overstory tree was found in 93% of highest suitability sites, but only in 43% medium and low suitability sites. As a midstory tree, it was only found in high suitability sites. *Andropogon* spp. was observed as dominant in 90% of the highest suitability sites, and in 72% of the medium and 50% of the lowest suitability sites. *Gaylussacia dumosa* was dominant in 62% of the highest suitability sites, 18% of the medium suitability sites, and 25% of the lowest suitability sites. *Vaccinium myrsinites* was found in 69% of the highest suitability sites, 55% of the medium and 31% of the lowest suitability sites. *Tephrosia virginiana* was found in 45% of the highest suitability sites, 9% of the medium sites, and 13% of the lowest. *Lyonia ligustrina* and *Lyonia mariana* were only observed as dominants in highest suitability sites.

4.4 Discussion

When assessed solely by the AUC score, this habitat suitability model performed very well; however, the goal of finding new populations of *Schwalbea americana* was not satisfied. It has been reported that habitat suitability models for rare species often result in high AUC values that might (Franklin et al., 2009) or might not accurately portray the model's efficacy (Breiner et al., 2015). On one hand, a model could perform better for rare species because they could be rare due to highly specific niches, which could be identified by a model from few occurrence points (Franklin et al., 2009). On the other hand, a model might score a high AUC simply as an artifact of the way the model was created. Models score higher by correctly predicting withheld occupations of the species across pixels, and for rare species, most pixels will be predicted to not contain the species, which might be true, but might not create a very effective model overall (Lawson et al., 2013; Sofaer et al., 2019). Solely relying on AUC as a measure of model success might thereby be flawed. This is why testing models' accuracy in the field is so important.

One might assess the current model as having failed due to its inability to locate new populations of Schwalbea. For rare plants, however, finding the target species is not guaranteed, even with a strong model. Boetsch et al. (2003) and McCune (2016) point out that when modeling habitat for rare plants, not finding the target species could be a result of factors such as habitat fragmentation, dispersal limitations, or historical events rather than model viability. It must also be emphasized that Maxent modeling does not predict species occurrence, but rather predicts the probability that individual pixels will contain suitable habitat for the species. Additionally, searches occurred when Schwalbea was seeding, not flowering, which could have made finding individuals difficult, even if they were present.

Even when a model fails to locate the target species, it can still provide useful information. Sometimes a rare species might not be found with the model, but the habitat surveyed is still judged to be suitable (van Manen et al., 2002; Williams et al., 2009; McCune, 2019). Such models can elucidate valuable information about environmental variables important for the species (McCune, 2019). For instance, the present model contains information about how Schwalbea responds to changing measurements of seven environmental variables. This information could be used in the creation of future habitat suitability models and to better understand species ecology. While no new Schwalbea populations were located, the habitat classified as most suitable by the model did consist of predominantly upland longleaf forests with nearby wetlands or rivers. Many species one would expect to find near Schwalbea were growing at the sites visited, including *Pinus palustris, Vaccinium myrsinites,* and *Gaylussacia dumosa*.

A common problem observed during surveying was that sites that seemed to contain vegetation consistent with Schwalbea habitat were disturbed to such an extent that the habitat no longer seemed suitable overall. This was noted for a third of the high suitability sites. Fire suppression, or too infrequent fire, can seriously degrade this rare plant's habitat. Even some of the known Schwalbea populations had not been burned with enough regularity to induce flowering in Schwalbea or the fire-dependent *A. beyrichiana*. In fact, fire-suppression is one documented reason for the species' decline (USFWS, 2018). Models that fail to include critical predictor variables will perform inadequately in locating unrecorded populations (Franklin et al., 2008; McCune, 2016). While this model attempted to account for missing fire data by including the LandFire variable Biophysical Setting, which takes historic fire regime into account, this was clearly not enough to represent current conditions. Future models for this endangered pyrophyte should include fire-interval data to produce more accurate suitability maps.

This model attempted to account for Schwalbea habitat across most of the Southeastern extent of its range. This was done in order to utilize as many occurrence points as possible and to capture as much information about the variability of habitats this species is found in as possible. Using more occurrences can improve model efficacy (van Proosdij et al., 2016; Behroozian et al., 2022). However, sometimes using a full suite of occurrences from across a broad geographic range can create a poor model since the model can fail to account for regional adaptations in the species. Indeed, the NMS ordination overlaid with States data indicates that there are clear groupings of sites based on states regardless of suitability, and that these groupings have less overlap than the Suitability overlay. NC and SC sites overlapped substantially, and Florida and Georgia sites did as well, but the NC-SC and FL-GA groups did not overlap much. These patterns in sites that fall outside of the suitability ranking could impact the overall effectiveness of the model. Furthermore, because of the size of the model, coarser resolution rasters had to be used in order for the model to run. It is possible that a model with 1 km^2 resolution was simply too coarse to capture the appropriate information for habitat classification, especially since Schwalbea is a species of ecotones and at least in the northern part of its range, might rely on microsite variation (Kelly & Denhof, 2022). Future models should take the grouping of SC-NC and GA-FL sites into account in order to create a more spatially explicit model with the capacity to account for regional adaptations. Future models should also be built with finer-resolution environmental rasters.

Some researchers have found that explicitly including species co-occurrence data in the habitat suitability modeling process can create more robust models (Baumberger et al., 2012; Gogol-Prokurat, 2014; McCune, 2016; Zhang et al., 2020; Meyer et al., 2022). Since researchers have reported the importance of community data in assessing models (McCune, 2019), rather than emphasizing presence or absence of the target species alone, incorporating this information could strengthen models for rare plants. While some of the common species associated with Schwalbea populations were found at sites classified as high suitability, explicitly including community data into the model might improve accuracy further. It could also improve model usefulness for locating sites for outplanting (Meyer et al., 2022).

Incorporating site surveys with model building is crucial in the iterative process of building habitat suitability models for rare species (McCune, 2019; Behroozian et al., 2022). The information gleaned from this modeling indicates that precipitation data is important for modeling Schwalbea habitat across its range. It also indicates that mean monthly ranges in temperature above 13° C is too much for the species, implying the necessity of a certain level of stability. Changes in precipitation and temperature will be more likely under ongoing global climate change. Future Schwalbea models should take this into account when modeling potential habitat. Information about changes that have already occurred in temperature and precipitation should be incorporated into models assessing population viability as they might explain declining trends across the range.

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Appendix.

Table A1. Site means for soil measurements. These measures pertain to pH (a), element concentration (b), and texture (c) measured at five *Schwalbea americana* sites at Ichauway.

a) pH and lime buffer capacity.

Variable	**Jericho**	**Parmalee**	**Pond 32**	**Rhexia 2**	**Rhexia 4**
LBC.eq (ppm CaCo$_3$/pH)	979	901	1004.5	1122.333	1010.000
pH	5.21	5.24	5.1	5.08	5.083

b) Element levels and plant-available nitrogen.

Variable	**Jericho**	**Parmalee**	**Pond 32**	**Rhexia 2**	**Rhexia 4**
Al (ppm)	5482	3803.333	3948.5	4894.667	3348.333
B (ppm)	2.28	1.103	1.17	1.9	1.043
Ca (ppm)	443.333	303.667	299	311.333	224
Cr (ppm)	4.377	2.5	2.73	4.03	2.313
Cu (ppm)	2.79	2.5	2.5	2.5	2.5
Fe (ppm)	2857.333	1774.667	1700.5	3380	1460.333
K (ppm)	52.13333	40.433	35.05	42.1	38.933
Mg (ppm)	165	119.267	115.95	127.733	100.733
Mn (ppm)	261.5	184.633	139.2	132.833	78.7
Na (ppm)	25	25	25	25	26.367
Ni (ppm)	2.763	1.117	1.33	1.9	1.487
P (ppm)	55.1	38.967	43.25	52.067	39.333
Pb (ppm)	5.52	3.66	3.965	5.063	4.127
S (ppm)	54.667	37.367	46.25	62.5	52
Zn (ppm)	3.58	2.5	2.5	4.847	2.5
NO3.N (mg/kg)	0.22	0.20	0.205	0.203	0.197

c.) Soil texture and organic carbon.

Variable	**Jericho**	**Parmalee**	**Pond 32**	**Rhexia 2**	**Rhexia 4**
OM- Organic Matter (%)	2.88	2.27	2.665	3.297	2.440
Sand (%)	79	83.2	81.7	80.967	82.967
Silt (%)	15.67	13.37	15.2	15.6	14.567
Clay (%)	5.41	3.44	3.12	3.413	2.400
TOC – Total Organic Carbon (%)	1.53	1.28	1.315	1.893	1.273

Table A2. Site comparison test results for soil measurements. Site comparison test results for soil variables measured at five *Schwalbea americana* sites at Ichauway. Kruskal-Wallis tests were used for non-normally distributed data, and ANOVAs were utilized for normally distributed data.

Variable	**df**	**F-value (ANOVA) or H-value (Kruskal-Wallis)**	**p-value**	**Test**
Sand	(4,9)	8.326	0.004	ANOVA
Silt	(4,9)	5.535	0.016	ANOVA
Clay	4	5.614	0.23	Kruskal-Wallis
LBCeq	(4,9)	2.11	0.162	ANOVA
pH	(4,9)	0.564	0.695	ANOVA
NO3.N	4	3.479	0.481	Kruskal-Wallis
OM.3	(4,9)	2.738	0.097	ANOVA
TOC	(4,9)	1.554	0.267	ANOVA
Al	(4,9)	7.03	0.008	ANOVA
B	4	9.924	0.042	Kruskal-Wallis
Ca	(4,9)	3.36	0.061	ANOVA
Cr	(4,9)	8.012	0.005	ANOVA
Cu	4	7.897	0.095	Kruskal-Wallis
Fe	(4,9)	12.36	0.001	ANOVA
K	(4,9)	1.62	0.251	ANOVA
Mg	(4,9)	9.461	0.003	ANOVA
Mn	(4,9)	4.108	0.037	ANOVA
Na	4	3.667	0.453	Kruskal-Wallis
Ni	4	11.015	0.026	Kruskal-Wallis
P	(4,9)	4.613	0.027	ANOVA
Pb	4	9.924	0.041	Kruskal-Wallis
S	(4,9)	(4,9)	0.0156	ANOVA
Zn	4	11.785	0.019	Kruskal-Wallis

Table A3**. **Fungal groups identified in** **Schwalbea americana** **roots.

Classes	**Orders**	**Families**	**Genera**
Agaricomycetes	Agaricales	Agaricaceae	Alternaria
Dothideomycetes	Atheliales	Amanitaceae	Amanita
Endogonomycetes	Auriculariales	Aspergillaceae	Arcopilus
Eurotiomycetes	Boletales	Atheliaceae	Aspergillus
Geminibasidiomycetes	Cantharellales	Boletaceae	Asterostroma
Geoglossomycetes	Capnodiales	Bulleribasidiaceae	Aureobasidium
Glomeromycetes	Chaetosphaeriales	Ceratobasidiaceae	Capronia

Leotiomycetes	Chaetothyriales	Chaetomellaceae	Cenococcum
Microbotryomycetes	Coniochaetales	Chaetomiaceae	Ceratobasidium
Mortierellomycetes	Corticiales	Chaetosphaeriaceae	Cladosporium
Orbiliomycetes	Diaporthales	Cladosporiaceae	Clavulina
Pezizomycetes	Dothideales	Clavariaceae	Coniochaeta
Rozellomycotina	Eurotiales	Clavulinaceae	Cortinarius
Saccharomycetes	Filobasidiales	Coniochaetaceae	Curvularia
Sordariomycetes	Geastrales	Corticiaceae	Desmazierella
Tremellomycetes	Geminibasidiales	Cortinariaceae	Devriesia
Umbelopsidomycetes	Geoglossales	Debaryomycetaceae	Diaporthe
	Glomerales	Dermateaceae	Echria
	Helotiales	Diaporthaceae	Epicoccum
	Hypocreales	Didymellaceae	Fusarium
	Hysteriales	Didymosphaeriaceae	Geminibasidium
	Leucosporidiales	Dothideaceae	Geoglossum
	Magnaporthales	Filobasidiaceae	Hannaella
	Mortierellales	Geminibasidiaceae	Hyaloscypha
	Myrmecridiales	Geoglossaceae	Hyphodontia
	Ophiostomatales	Glomeraceae	Inocybe
	Orbiliales	Gloniaceae	Kalmusia
	Pezizales	Herpotrichiellacea	Kurtzmaniella
	Pleosporales	Hyaloscyphaceae	Lachnum
	Polyporales	Hypocreaceae	Lactarius
	Russulales	Inocybaceae	Lentinus
	Saccharomycetales	Lachnocladiaceae	Leohumicola
	Sebacinales	Lasiosphaeriaceae	Lycoperdon
	Sordariales	Lindgomycetaceae	Marasmius
	Sporidiobolales	Lophiotremataceae	Meyerozyma
	Thelephorales	Lycoperdaceae	Mollisia
	Tremellales	Magnaporthaceae	Mortierella
	Trichosphaeriales	Marasmiaceae	Mycena
	Umbelopsidales	Massarinaceae	Mycosymbioces
	Venturiales	Mortierellaceae	Myrmecridium
	Xylariales	Mycenaceae	Naganishia
		Mycosphaerellaceae	Neurospora
		Myrmecridiaceae	Nigrospora
		Myxotrichaceae	Ochroconis
		Nectriaceae	Oidiodendron

		Ophiostomataceae	Papiliotrema
		Orbiliaceae	Paraphaeosphaeria
		Periconiaceae	Penicillium
		Phaeosphaeriaceae	Periconia
		Pholiota	Pestalotiopsis
		Pleosporaceae	Pezicula
		Polyporaceae	Pilidium
		Pyronemataceae	Plectania
		Rhynchogastremataceae	Preussia
		Russulaceae	Pseudophialophora
		Saccotheciaceae	Rachicladosporium
		Sarcoscyphaceae	Rhizophagus
		Sebacinaceae	Rhizosphaera
		Serendipitaceae	Rhodosporidiobolus
		Sordariaceae	Rhodotorula
		Sporidiobolaceae	Seiridium
		Sporocadaceae	Serendipita
		Sporormiacea	Sporobolomyces
		Stachybotryaceae	Stagonospora
		Strophariaceae	Talaromyces
		Sympoventuria	Thielavia
		Teratosphaeriaceae	Thozetella
		Thelephoraceae	Tomentella
		Trichocomaceae	Toxicocladosporium
		Trichosphaeriaceae	Trichoderma
		Umbelopsidaceae	Tylospora
			Umbelopsis
			Xenosonderhenia

Table A4. Fungal genera identified in Schwalbea roots. Fungal genera identified in *Schwalbea americana* root samples via ITS region amplification and sequencing.

Genus	**Ecology**	**Effect on Plants**
Alternaria	Genus includes saprophytes, endophytes and pathogens (Meena et al., 2017)	mixed
Amanita	Mostly ECM fungi (Hess & Pringle, 2014)	beneficial
Arcopilus	Known to exist as endophytes, providing defenses to host against disease (Tavares et al., 2022)	beneficial
Aspergillus	Mainly saprobes (Pangging et al., 2022)	neutral
Asterostroma	Ecology not widely described	unknown

Aureobasidium	Black yeast described as an extremotolerant (Wang et al., 2019) At least some species produce plant growth promoting chemicals (Sun et al., 2019)	neutral-beneficial
Capronia	Mostly saprobic, thermotolerant (Phukhamsakda et al., 2022)	neutral
Cenococcum	At least some are tolerant of water stress and convey this to plants through ectomycorrhizal symbiosis (Fernandez & Koide, 2013) Predominantly an ectomycorrhizal genus (Hyde et al., 2013)	beneficial
Ceratobasidium	Mycorrhizal with orchids, but also includes plant pathogens as well as biocontrol agents (Mosquera-Espinosa et al., 2013)	mixed
Cladosporium	Common endophytes, plant pathogens (Bensch et al., 2012)	mixed
Clavulina	Largely ectomycorrhizal (Henkel et al., 2011)	beneficial
Coniochaeta	Endophytes, saprobes, pathogens (Damm et al., 2010)	mixed
Cortinarius	Ectomycorrhizal (Bödeker et al., 2014)	beneficial
Curvularia	Largely plant pathogens (Cui et al., 2020)	harmful
Desmazierella	Important for decomposition (MicrobeWiki, 2016)	neutral
Devriesia	Heat-resistant fungi (Kikoku et al., 2008) and causes sooty blotch (Li et al., 2013)	mixed
Diaporthe	At least some species are plant pathogens (Floyd & Malvick, 2022)	harmful
Echria	Not much information	unknown
Epicoccum	Can be endophytic and release antifungal and antibacterial compounds, but also known pathogens (Del Frari et al., 2020)	mixed
Fusarium	Major plant pathogen (Brown et al., 2022)	harmful
Geminibasidium	Saprobic xerotolerant and heat-resistant fungi (Pulido-Chavez 2021)	neutral
Geoglossum	Not much information about plant interactions	unknown
Hannaella	Not much information about plant interactions	unknown
Hyaloscypha	Decomposers mainly (Quijada et al., 2017)	neutral
Hyphodontia	Saprobes (Wang et al., 2021)	neutral
Inocybe	Ectomycorrhizal (Patocka et al., 2021)	beneficial
Kalmusia	Uncertain relationship with plants	unknown
Kurtzmaniella	Uncertain relationship with plants	unknown
Lachnum	Common root fungi (Bizabani & Dames, 2015)	neutral-beneficial
Lactarius	Associate with trees and shrubs (Vieira et al., 2014)	neutral
Lentinus	Wood-decaying (Karunarathna et al., 2011)	neutral
Leohumicola	Ericaceous mycorrhizae (Baba & Hirose, 2020)	neutral-beneficial
Lycoperdon	Uncertain relationship with plants	unknown
Marasmius	Uncertain relationship with plants	unknown
Meyerozyma	Some yeasts of this genus have been found to produce compounds favorable for siderophore production,	neutral-beneficial

	helpful in plants' ability to tolerate oxidative stress (de Lima Targino et al., 2022)	
Mollisia	Endophytes common (Tanney & Seifert, 2020)	neutral-beneficial
Mortierella	Can be saprobes or root endophytes enhancing plant growth (University of Florida, 2021)	neutral-beneficial
Mycena	Exist on a continuum from saprobic to endophytic (Thoen et al., 2020)	neutral-beneficial
Mycosymbioces	Not much information	unknown
Myrmecridium	Not much information, but at least some species endophytic (Tan et al., 2012)	neutral-beneficial
Naganishia	Not much information	unknown
Neurospora	Fungi found on plant material after fires (Perkins & Turner, 1988)	neutral
Nigrospora	Pathogens, endophytes, and saprobes (Hao et al., 2020)	mixed
Ochroconis	Mostly saprobes (Machouart et al., 2014)	neutral
Oidiodendron	Ericaceous endophytes (Hambleton et al., 1998)	neutral
Papiliotrema	Yeast promoting growth in plants (Labancová et al., 2022), and presence can protect against disease through competition and nutritional supplementation (Liu et al., 2021)	beneficial
Paraphaeosphaeria	Plant pathogens, biocontrol agents, beneficial endophytes and bioremediators (Baroncelli et al., 2020)	mixed
Penicillium	Large role in decomposition, but also a plant pathogen (Visagie et al., 2014)	mixed
Periconia	Endophytes, saprophytes, and pathogens (Markovskaja & Kačergius, 2014)	mixed
Pestalotiopsis	Mainly pathogenic fungi (Maharachchikumbura et al., 2014)	harmful
Pezicula	Saprobes, endophytes, weak pathogens when plant hosts are under stress (Chen et al., 2016)	mixed
Pilidium	Phytopathogenic genus (Marin-Felix et al., 2017)	harmful
Plectania	Not much information	unknown
Preussia	Endophytes (Massimo et al., 2015)	beneficial
Pseudophialophora	Root parasites (Luo et al., 2015)	harmful
Rachicladosporium	At least one species of endolithic, rock-dwelling, fungus (Coleine et al., 2017)	neutral
Rhizophagus	Arbuscular mycorrhizal fungi (Cartabia et al., 2021)	beneficial
Rhizosphaera	Fungal blight (Ash Kanner & Grabowski, 2019)	harmful
Rhodosporidiobolus	Useful for biotechnology (Polburee & Limtong, 2020)	neutral
Rhodotorula	Emerging pathogen for humans (Wirth & Goldani, 2012)	neutral
Seiridium	Plant pathogens (Bonthond et al., 2018)	harmful
Serendipita	At least some species are root endophytes with positive agricultural applications, potential for plant growth enhancement (Shekhawat et al., 2021), and also some orchid mycorrhizae (Oktalira et al., 2021)	beneficial
Sporobolomyces	Not much information about interactions with plants	unknown

Stagonospora	Pathogens on cereals (Cunfer & Ueng, 1999)	harmful
Talaromyces	Not much known about plant interactions	unknown
Thielavia	Endophytes, phytopathogens, or neutral. Can tolerate high temperatures and pH (Sabrin et al., 2022)	mixed
Thozetella	Not much information	unknown
Tomentella	Ectomycorrhizae (Alvarez-Manjarrez et al., 2016)	beneficial
Toxicocladosporium	Pathogens to saprobes, epiphytes and endophytes (Bakhshi et al., 2022)	mixed
Trichoderma	Saprobes and biocontrol agents against plant pathogens (Kubicek et al., 2008)	neutral-beneficial
Tylospora	Ectomycorrhizal fungi (Southam et al., 2022)	beneficial
Umbelopsis	Mostly saprobes, but also root endophytes (Sukdeo et al., 2018).	neutral-beneficial
Xenosonderhenia	Not much is known	unknown

Table A5. Species list (Ichauway). Species list of species observed during vegetation sampling for indicator species analysis and functional group analysis. WIS refers to Wetland Indicator Status (FAC=Facultative, FACU=Facultative Upland, FACW=Facultative Wetland, OBL=Obligate Wetland, UPL=Upland).

Species Code	**Genus**	**Species**	**Authority**	**Common name**	**Growth Form**	**WIS**	**Family**
ACGR	*Acalypha*	*gracilens*	A. Gray	Shortstalk copperleaf	Forb	FAC	Euphorbiaceae
ACRU	*Acer*	*rubrum*	Linnaeus	Eastern red maple	Tree	FAC	Aceraceae
AGFA	*Agalinis*	*fasciculata*	(Elliott) Rafinesque	Beach false foxglove	Forb	FAC	Orobanchaceae
AGIN	*Agrimonia*	*incisa*	Torrey & A. Gray	Pineland agrimony	Forb	FAC	Rosaceae
AMAT	*Ambrosia*	*artemisiifolia*	Linnaeus	Common ragweed	Forb	FACU	Asteraceae
AMMU	*Amphicarpum*	*muehlenbergianum*	(J.A. Schultes) A.S. Hitchcock	Florida peanut-grass, blue maiden-cane	Graminoid	FACW	Poaceae
AN01	*Andropogon*	*sp.*	--	--	Graminoid	--	Poaceae
ANVI	*Anthenantia*	*villosa*	(Michaux) Palisot de Beauvois	Green silkyscale	Graminoid	UPL	Poaceae
ARAR	*Aronia*	*arbutifolia*	(Linnaeus) Persoon	Red chokeberry	Shrub	FACW	Rosaceae
ARBE	*Aristida*	*beyrichiana*	Trinius & Ruprecht	Southern wiregrass	Graminoid	FAC	Poaceae
ARG1	*Aristida*	*sp.*	--	Former Aristida purpurascens complex	Graminoid	--	Poaceae
ARPU	*Aristida*	*purpurascens*	Poiret	Arrowfeather	Graminoid	UPL	Poaceae
ASGR	*Asemeia*	*grandiflora*	(Walter) Small	Showy milkwort	Forb	OBL	Polygalaceae
ASSP	*Asimina*	*spatulata*	(Kral) D.B. Ward	Slimleaf pawpaw	Shrub	FACU	Annonaceae
ASVE	*Asclepias*	*verticillata*	Linnaeus	Whorled milkweed	Forb	FACU	Apocynaceae

BUFL	*Buchnera*	*floridana*	Gandoger	Savanna bluehearts, florida bluehearts	Forb	FAC	Orobanchaceae
CAGU	*Carex*	*glaucescens*	Elliott	Blue sedge, southern waxy sedge	Graminoid	OBL	Cyperaceae
CEMI	*Ceanothus*	*microphyllus*	Michaux	Littleleaf buckbrush	Subshrub	UPL	Rhamnaceae
CEVI	*Centrosema*	*virginianum*	(Linnaeus) Bentham	Spurred butterfly pea	Vine	UPL	Fabaceae
CHFA	*Chamaecrista*	*fasciculata*	(Michaux) Greene	Common partridge-pea	Forb	FACU	Fabaceae
CHMA	*Chrysopsis*	*mariana*	(Linnaeus) Elliott	Maryland golden-aster	Forb	UPL	Asteraceae
CHNC	*Chamaecrista*	*nictitans*	(Linnaeus) Moench	Common sensitive-plant	Forb	FACU	Fabaceae
CHNI	*Chasmanthium*	*nitidum*	(Baldwin) Yates	Shiny spanglegrass	Graminoid	FACW	Poaceae
CHTO	*Chaptalia*	*tomentosa*	Ventenat	Sunbonnets, pineland daisy, night-nodding bog-dandelion, woolly sunbonnets	Forb	FACW	Asteraceae
CLMA	*Clitoria*	*mariana*	Linnaeus	Butterfly pea, she-pea	Forb	FACU	Fabaceae
CNST	*Cnidoscolus*	*stimulosus*	(Michaux) Engelmann & A. Gray	Spurge-nettle, tread-softly, finger-rot, bull-nettle	Forb	UPL	Euphorbiaceae
CRAR	*Croton*	*argyranthemus*	Michaux	Silver croton, sandhill croton, healing croton	Forb	UPL	Euphorbiaceae
CRCA	*Croton*	*capitatus*	Michaux	Woolly croton, hogwort,	Forb	UPL	Euphorbiaceae

				capitate croton, goatweed			
CRCR	*Crocanthemum*	*carolinianum*	(Walter) Spach	Carolina sunrose	Forb	UPL	Cistaceae
CRLS	*Crataegus*	*lassa*	Beadle	Hawthorn	Shrub/Tree	FAC	Rosaceae
CRMA	*Crataegus*	*marshallii*	Eggleston	Parsley hawthorn, parsley haw	Shrub	FAC	Rosaceae
CRPU	*Crotalaria*	*purshii*	A.P. de Candolle	Coastal plain rattlebox, pursh's rattlebox	Forb	UPL	Fabaceae
CRRO	*Crotalaria*	*rotundifolia*	Walter ex J.F. Gmelin	Low rattlebox, rabbitbells	Forb	FACU	Fabaceae
CRRS	*Crocanthemum*	*rosmarinifolium*	(Pursh) Janchen	Rosemary sunrose	Forb	UPL	Cistaceae
CYFI	*Cyperus*	*filiculmis*	Vahl	Southeastern flatsedge	Graminoid	UPL	Cyperaceae
DE01	*Desmodium*	*sp.*	Desv.	--	Forb	--	Fabaceae
DE02	*Desmodium*	*spp.*	Desv.	--	Forb	--	Fabaceae
DECI	*Desmodium*	*ciliare*	(Muhlenberg ex Willdenow) A.P. de Candolle	Hairy small-leaved tick tre-foil	Forb	UPL	Fabaceae
DELI	*Desmodium*	*lineatum*	A.P. de Candolle	Matted tick-trefoil	Forb	UPL	Fabaceae
DEST	*Desmodium*	*strictum*	(Pursh) A.P. de Candolle	Pineland tick-trefoil, pinebarren tick-trefoil	Forb	UPL	Fabaceae
DI01	*Dichanthelium*	*sp.*	(Hitchc. & Chase) Gould	--	Graminoid	--	Poaceae
DIAG	*Dichanthelium*	*angustifolium*	(Elliott) Gould	Narrowleaf witchgrass	Graminoid	UPL	Poaceae
DISP	*Dichanthelium*	*sphaerocarpon*	(Elliott) Gould	Round-fruited witchgrass	Graminoid	FACU	Poaceae
DIST	*Dichanthelium*	*strigosum*	(Muhlenberg ex Elliott) Freckmann	Rough-hairy witchgrass	Graminoid	FAC	Poaceae

DITN	*Dichanthelium*	*tenue*	(Muhlenberg) Freckmann & Lelong.	White-edged witchgrass.	Graminoid	FAC	Poaceae
DIVM	*Dichanthelium*	*villosissimum*	(Nash) Freckmann	White-haired witchgrass	Graminoid	FACU	Poaceae
DIVR	*Diospyros*	*virginiana*	Linnaeus	American persimmon, possumwood	Tree	FAC	Ebenaceae
DIWR	*Dichanthelium*	*wrightianum*	(Lamson-Scribner) Freckmann	Wright's witchgrass	Graminoid	FACW	Poaceae
DYOB	*Dyschoriste*	*oblongifolia*	(Michaux) Kuntze	Blue twinflower, pineland dyschoriste	Forb	UPL	Acanthaceae
EB01	*Euphorbia*	*sp.*	L.	--	Forb	--	Euphorbiaceae
EB02	*Euphorbia*	*spp.*	Linnaeus	--	Forb	--	NA
ELEL	*Elephantopus*	*elatus*	Bertoloni	Southern elephant's-foot	Forb	FACU	Asteraceae
ENSE	*Endodeca*	*serpentaria*	(Linnaeus) Rafinesque	Turpentine-root, virginia snakeroot, serpent birthwort	Forb	FACU	Aristolochiaceae
ERVE	*Erigeron*	*vernus*	(Linnaeus) Torrey & A. Gray	Whitetop fleabane	Forb	OBL	Asteraceae
ERYS	*Eryngium*	*yuccifolium*	Michaux A. Gray ex Coulter & Rose	Southern rattlesnake-master	Forb	FAC	Apiaceae
EUCA	*Eupatorium*	*capillifolium*	(Lamarck) Small	Common dog-fennel, yankeeweed, cypressweed	Forb	FACU	Asteraceae
EUCL	*Euthamia*	*caroliniana*	(Linnaeus) Greene ex Porter & Britton	Carolina goldentop	Forb	FAC	Asteraceae
EUCO	*Eupatorium*	*compositifolium*	Walter	Coastal dog-fennel, yankeeweed	Forb	FAC	Asteraceae

EUHS	*Euphorbia*	*hyssopifolia*	Linnaeus	Hyssopleaf sandmat	Forb	FAC	Euphorbiaceae
EUHY	*Eupatorium*	*hyssopifolium*	Linnaeus	Hyssopleaf eupatorium	Forb	FAC	Asteraceae
EULU	*Eupatorium*	*leucolepis*	(A.P. de Candolle) Torrey & A. Gray	Savanna eupatorium, justiceweed	Forb	FACW	Asteraceae
EUPU	*Euphorbia*	*pubentissima*	Michaux	Southeastern flowering spurge	Forb	FAC	Euphorbiaceae
EURO	*Eupatorium*	*rotundifolium*	Linnaeus	Common roundleaf eupatorium	Forb	FAC	Asteraceae
EUSE	*Eupatorium*	*semiserratum*	A.P. de Candolle	Smallflower throughwort	Forb	FACW	Asteraceae
GA01	*Galium*	*sp.*	Linnaeus	--	Forb	--	Rubiaceae
GADU	*Gaylussacia*	*dumosa*	(Andrews) Torrey & A. Gray	Southern dwarf huckleberry	Shrub	FAC	Ericaceae
GAER	*Galactia*	*erecta*	(Walter) Vail	Erect milkpea	Forb	UPL	Fabaceae
GAMN	*Galactia*	*minor*	W.H. Duncan.	Little milkpea	Forb	UPL	Fabaceae
GANA	*Gaylussacia*	*nana*	(A. Gray) Small	Dwarf dangleberry	Shrub	FAC	Ericaceae
GAPI	*Galium*	*pilosum*	Aiton	Hairy bedstraw	Forb	FAC	Rubiaceae
GAPU	*Gamochaeta*	*purpurea*	(Linnaeus) Cabrera	Spoonleaf purple everlasting	Forb	UPL	Asteraceae
GARE	*Galactia*	*regularis*	(Linnaeus) britton, sterns, & poggenburg		Vine	UPL	Fabaceae
GEOB	*Geobalanus*	*oblongifolius*	(Michaux) Small	Gopher-apple, ground-oak	Subshrub	UPL	Chrysobalanaceae
GESE	*Gelsemium*	*sempervirens*	(Linnaeus) St. Hilaire	Carolina jessamine	Vine	FAC	Gelsemiaceae
GYAM	*Gymnopogon*	*ambiguus*	(Michaux) Britton, Sterns, & Poggenburg	Eastern skeleton grass, eastern beard grass	Graminoid	UPL	Poaceae

GYBR	*Gymnopogon*	*brevifolius*	Trinius	Pineland skeleton grass, pineland beard grass	Graminoid	FACU	Poaceae
HAQU	*Habenaria*	*quinqueseta*	(Michaux) A. Eaton	Michaux’s orchid	Forb	FACW	Orchidaceae
HEAN	*Helianthus*	*angustifolius*	Linnaeus	Narrowleaf sunflower	Forb	FACW	Asteraceae
HEHI	*Helianthus*	*hirsutus*	Rafinesque	Hairy sunflower	Forb	UPL	Asteraceae
HERA	*Helianthus*	*radula*	(Pursh) Torrey & A. Gray	Roundleaf sunflower, rayless sunflower	Forb	FAC	Asteraceae
HETE	*Hexasepalum*	*teres*	(Walter) J.H. Kirkbride	Poorjoe	Forb	FACU	Rubiaceae
HIAC	*Hibiscus*	*aculeatus*	Walter	Savanna hibiscus, comfort-root	Forb	FACW	Malvaceae
HIGR	*Hieracium*	*gronovii*	Linnaeus	Beaked hawkweed, queendevil	Forb	UPL	Asteraceae
HOPR	*Houstonia*	*procumbens*	(Walter ex J.F. Gmelin) Standley	Creeping bluet, fairy-footprints, roundleaf bluet, innocence	Forb	FACU	Rubiaceae
HY01	*Hypericum*	*sp.*	Linnaeus	--	Subshrub	--	Hypericaceae
HYCR	*Hypericum*	*crux-andreae*	(Linnaeus) Crantz	St. Andrew's cross, st. Peter's-wort	Subshrub	FACW	Hypericaceae
HYCU	*Hypoxis*	*curtissii*	Rose	Swamp stargrass, curtiss’s stargrass	Forb	FACW	Hypoxidaceae
HYHY	*Hypericum*	*hypericoides*	(Linnaeus) Crantz	St. Andrew's cross	Subshrub	FAC	Hypericaceae

HYSU	*Hypericum*	*suffruticosum*	W.P. Adams & Robson	Pineland st. John's-wort	Subshrub	FACW	Hypericaceae
HYWR	*Hypoxis*	*wrightii*	(Baker) Brackett	Bristleseed stargrass	Forb	FACW	Hypoxidaceae
ILGL	*Ilex*	*glabra*	(Linnaeus) A. Gray	Little gallberry, inkberry	Shrub	FACW	Aquifoliaceae
ILMY	*Ilex*	*myrtifolia*	Walter	Myrtle holly	Shrub	FACW	Aquifoliaceae
IPPA	*Ipomoea*	*pandurata*	(Linnaeus) G.F.W. Meyer	Wild sweet potato, manroot, man-of-the-earth	Vine	FACU	Convolvulaceae
JULA	*Justicia*	*lanceolata*	(Chapman) Small		Forb	OBL	Acanthaceae
KEVE	*Kellochloa*	*verrucosa*	(Muhlenberg) Lizarazu, M.V. Nicola, & Scataglini	Warty panic grass	Graminoid	FACW	Poaceae
LE01	*Lechea*	*sp.*	Linnaeus	--	Forb	--	Cistaceae
LEAN	*Lespedeza*	*angustifolia*	(Pursh) Elliott	Narrow-leaved lespedeza	Forb	FAC	Fabaceae
LEHE	*Leersia*	*hexandra*	Swartz	Southern cutgrass	Graminoid	OBL	Poaceae
LEMI	*Lechea*	*minor*	Linnaeus	Thymeleaf pinweed	Forb	UPL	Cistaceae
LERE	*Lespedeza*	*repens*	(Linnaeus) W. Barton	Smooth trailing lespedeza, creeping lespedeza	Forb	UPL	Fabaceae
LIFC	*Linum*	*floridanum*	(Planchon) Trelease C.M. Rogers	Yellow-fruited yellow flax	Forb	FAC	Linaceae
LOPU	*Lobelia*	*puberula*	Michaux	Downy lobelia	Forb	FACW	Campanulaceae
LS01	*Lespedeza*	*sp.*	Michx.	--	Forb	--	Fabaceae

LULI	*Ludwigia*	*linearis*	Walter	Eastern narrowleaf seedbox	Forb	OBL	Onagraceae
LUVI	*Ludwigia*	*virgata*	Michaux	Savanna seedbox	Forb	OBL	Onagraceae
MEAC	*Mecardonia*	*acuminata*	(Walter) Small	Mecardonia, common axil-flower	Forb	FACW	Plantaginaceae
MIMI	*Mimosa*	*microphylla*	Dryander	Eastern sensitive-briar	Vine	UPL	Fabaceae
MISE	*Mitreola*	*sessilifolia*	(J.F. Gmelin) G. Don	Small-leaved miterwort	Forb	FACW	Loganiaceae
MOCE	*Morella*	*cerifera*	(Linnaeus) Small	Common wax-myrtle, southern bayberry	Shrub	FAC	Myricaceae
MOCE	*Morella*	*cerifera*	(Linnaeus) Small	Common wax-myrtle, southern bayberry	Shrub	FAC	Myricaceae
MURO	*Muscadinia*	*rotundifolia*	(Michaux) Small	Muscadine, scuppernong	Vine	FAC	Vitaceae
NEAR	*Nekemias*	*arborea*	(Linnaeus) J. Wen & Boggan	Peppervine	Vine	FAC	Vitaceae
PAPL	*Paspalum*	*plicatulum*	Michaux	Brownseed paspalum	Graminoid	FAC	Poaceae
PASE	*Paspalum*	*setaceum*	Michaux	Thin paspalum	Graminoid	FAC	Poaceae
PAVI	*Panicum*	*virgatum*	Linnaeus	Switchgrass	Graminoid	FAC	Poaceae
PHHE	*Physalis*	*heterophylla*	Nees	Clammy ground-cherry	Forb	UPL	Solanaceae
PICA	*Piriqueta*	*caroliniana*	(Walter) Urban	Carolina piriqueta	Forb	UPL	Turneraceae
PILU	*Pinguicula*	*lutea*	Walter	Yellow butterwort	Forb	OBL	Lentibulariaceae
PINE	*Pityopsis*	*nervosa*	(Willdenow) Dress		Forb	UPL	Asteraceae
POCY	*Polygala*	*cymosa*	Walter	Tall pinebarren milkwort	Forb	OBL	Polygalaceae

PONA	*Polygala*	*nana*	(Michaux) A.P. de Candolle	Dwarf milkwort, candyroot	Forb	FACW	Polygalaceae
POPG	*Polygala*	*polygama*	Walter	Bitter milkwort, racemed milkwort	Forb	FACU	Polygalaceae
POPR	*Polypremum*	*procumbens*	Linnaeus	Polypremum, rustweed, juniperleaf	Forb	FACU	Tetrachondraceae
PRPE	*Proserpinaca*	*pectinata*	Lamarck	Feathery mermaid-weed	Forb	OBL	Haloragaceae
PRSE	*Prunus*	*serotina*	Ehrhart	Eastern wild black cherry, bird cherry	Tree	FACU	Rosaceae
PTPS	*Pteridium*	*pseudocaudatum*	(Clute) Christenhusz	Southern bracken	Forb	FACU	Dennstaedtiaceae
PTPY	*Pterocaulon*	*pycnostachyum*	(Michaux) Elliott	Blackroot, pineland wingstem	Forb	FACU	Asteraceae
PYFL	*Pycnanthemum*	*flexuosum*	(Walter) Britton, Sterns, & Poggenburg	Savanna mint, savanna mountain-mint	Forb	FACW	Lamiaceae
QUFA	*Quercus*	*falcata*	Michaux	Spanish oak, southern red oak	Tree	FACU	Fagaceae
QUGE	*Quercus*	*geminata*	Small	Sand live oak	Tree	UPL	Fagaceae
QUHE	*Quercus*	*hemisphaerica*	Bartram ex Willdenow	Sand laurel oak, darlington oak	Tree	FACU	Fagaceae
QUIN	*Quercus*	*incana*	Bartram	Bluejack oak	Tree	UPL	Fagaceae
QUNI	*Quercus*	*nigra*	Linnaeus	Water oak, paddle oak	Tree	FAC	Fagaceae
QUVI	*Quercus*	*virginiana*	P. Miller	Live oak	Tree	FACU	Fagaceae
RH01	*Rhynchospora*	*sp.*	Vahl	--	Graminoid	--	Cyperaceae

RHAL	*Rhexia*	*alifanus*	Walter	Smooth meadow-beauty	Forb	FACW	Melastomataceae
RHCO	*Rhus*	*copallinum*	Linnaeus	Eastern winged sumac, eastern flameleaf sumac	Shrub	UPL	Anacardiaceae
RHDI	*Rhynchosia*	*difformis*	(Elliott) A.P. de Candolle		Vine	UPL	Fabaceae
RHMA	*Rhexia*	*mariana*	Michaux	Maryland meadow-beauty	Forb	FACW	Melastomataceae
RHRE	*Rhynchosia*	*reniformis*	A.P. de Candolle	Dollarweed, dollarleaf snoutbean	Forb	UPL	Fabaceae
RHTO	*Rhynchosia*	*tomentosa*	(Linnaeus) Hooker & Arnott	Erect snoutbean	Forb	UPL	Fabaceae
RHVI	*Rhexia*	*virginica*	Linnaeus	Virginia meadow-beauty, deergrass, handsome harry, wing-stem meadow-beauty	Forb	FACW	Melastomataceae
RUCA	*Ruellia*	*caroliniensis*	(J.F. Gmelin) Steudel	Carolina wild-petunia, common wild-petunia	Forb	FACU	Acanthaceae
RUCU	*Rubus*	*cuneifolius*	Pursh	Sand blackberry	Subshrub	FACU	Rosaceae
RUHN	*Rudbeckia*	*hirta*	Linnaeus (T.V. Moore) Perdue	Coastal plain black-eyed susan	Forb	FACU	Asteraceae
SAAL	*Sassafras*	*albidum*	(Nuttall) Nees	Sassafras	Tree	FACU	Lauraceae
SCAM	*Schwalbea*	*americana*	Linnaeus	Chaffseed	Forb	FAC	Orobanchaceae

SCCI	*Scleria*	*ciliata*	Michaux	Hairy nutrush	Graminoid	FAC	Cyperaceae
SCIT	*Scutellaria*	*integrifolia*	Linnaeus	Narrowleaf skullcap	Forb	FAC	Lamiaceae
SCTE	*Schizachyrium*	*tenerum*	Nees	Slender bluestem	Graminoid	UPL	Poaceae
SEOB	*Senna*	*obtusifolia*	(Linnaeus) H.S. Irwin & Barneby	Sicklepod, coffeeweed	Forb	FACU	Fabaceae
SETR	*Sericocarpus*	*tortifolius*	(Michaux) Nees	Twisted-leaf white-topped aster	Forb	UPL	Asteraceae
SIXE	*Sisyrinchium*	*xerophyllum*	Greene	Florida blue-eyed-grass	Forb	UPL	Iridaceae
SMBO	*Smilax*	*bona-nox*	Linnaeus	Stretchberry, fringed greenbriar, catbriar, tramp's-trouble	Vine	FAC	Smilacaceae
SMGL	*Smilax*	*glauca*	Walter	Whiteleaf greenbriar, wild sarsaparilla	Vine	FAC	Smilacaceae
SMRO	*Smilax*	*rotundifolia*	Linnaeus	Common greenbriar, bullbriar, horsebriar	Vine	FAC	Smilacaceae
SONU	*Sorghastrum*	*nutans*	(Linnaeus) Nash	Yellow indiangrass	Graminoid	FACU	Poaceae
SOOD	*Solidago*	*odora*	Aiton	Licorice goldenrod	Forb	UPL	Asteraceae
SOPI	*Sophronanthe*	*pilosa*	(Michaux) Small	Shaggy hedge-hyssop	Forb	FACW	Plantaginaceae
SOTO	*Solidago*	*tortifolia*	Elliott	Leafy pineywoods goldenrod	Forb	UPL	Asteraceae
SOVR	*Solidago*	*virgata*	Michaux	Wand goldenrod	Forb	OBL	Asteraceae
STAQ	*Stylisma*	*aquatica*	(Walter) Rafinesque	Water downflower	Vine	FACW	Convolvulaceae

STBI	*Stylosanthes*	*biflora*	(Linnaeus) Britton, Sterns, & Poggenburg	Pencil-flower	Forb	UPL	Fabaceae
STHU	*Stylisma*	*humistrata*	(Walter) Chapman	Southern dawnflower	Vine	UPL	Convolvulaceae
STUM	*Strophostyles*	*umbellata*	(Muhlenberg ex Willdenow) Britton	Perennial sand bean, perennial fuzzy bean	Vine	FAC	Fabaceae
SYAD	*Symphyotrichum*	*adnatum*	(Nuttall) Nesom		Forb	FACW	Asteraceae
SYCO	*Symphyotrichum*	*concolor*	(Linnaeus) Nesom	Eastern silvery aster	Forb	UPL	Asteraceae
SYDU	*Symphyotrichum*	*dumosum*	(Linnaeus) Nesom	Long-stalked aster	Forb	FAC	Asteraceae
TEFL	*Tephrosia*	*florida*	(F.G. Dietrich) C.E. Wood	Florida hoarypea, florida goat's-rue	Forb	UPL	Fabaceae
TESP	*Tephrosia*	*spicata*	(Walter) Torrey & A. Gray	Spiked hoarypea	Forb	UPL	Fabaceae
TEVI	*Tephrosia*	*virginiana*	(Linnaeus) Persoon	Virginia goat's-rue, devil's shoelaces	Forb	UPL	Fabaceae
TOPU	*Toxicodendron*	*pubescens*	P. Miller	Poison oak, southeastern poison oak	Subshrub	FACU	Anacardiaceae
TRDI	*Trichostema*	*dichotomum*	Linnaeus	Common blue curls	Forb	UPL	Lamiaceae
TROD	*Trilisa*	*odoratissima*	(J.F. Gmelin) Cassini	Deer's-tongue, vanilla-leaf	Forb	FACW	Asteraceae
TRSM	*Tragia*	*smallii*	Shinners	Gulf coast noseburn	Forb	UPL	Euphorbiaceae
TRUR	*Tragia*	*urens*	Linnaeus	Southeastern noseburn, wavyleaf noseburn, sandhill noseburn	Forb	UPL	Euphorbiaceae

Unk102	--	--	--	--	Graminoid	--	--
Unk109	--	--	--	--	Forb	--	--
Unk111	--	--	--	--	Graminoid	--	--
Unk114	--	--	--	--	Graminoid	--	--
Unk116	--	--	--	--	Forb	--	--
Unk125	--	--	--	--	Forb	--	--
UNK134	--	--	--	--	Graminoid	--	--
Unk136	--	--	--	--	Forb	--	--
Unk143	--	--	--	--	Forb	--	--
Unk145	--	--	--	--	Forb	--	--
Unk154	--	--	--	--	Graminoid	--	--
Unk156	--	--	--	--	Forb	--	--
Unk167	--	--	--	--	Shrub	--	--
Unk169	--	--	--	--	Forb	--	--
Unk170	--	--	--	--	Graminoid	--	--
Unk172	--	--	--	--	Forb	--	--
Unk173	--	--	--	--	Graminoid	--	--
Unk174	--	--	--	--	Graminoid	--	--
Unk177	--	--	--	--	Forb	--	--
Unk180	--	--	--	--	Graminoid	--	--
Unk184	--	--	--	--	Graminoid	--	--
Unk186	--	--	--	--	Forb	--	--
Unk187	--	--	--	--	Forb	--	--
Unk37	--	--	--	--	Shrub	--	--
Unk43	--	--	--	--	Forb	--	--
Unk56	--	--	--	--	Forb	--	--
Unk59	--	--	--	--	Forb	--	--
Unk62	--	--	--	--	Forb	--	--
Unk82	--	--	--	--	Forb	--	--
Unk83	--	--	--	--	Forb	--	--
Unk86	--	--	--	--	Forb	--	--

Unk89	--	--	--	--	Graminoid	--	--
Unk97	--	--	--	--	Graminoid	--	--
Unk99	--	--	--	--	Forb	--	--
VAEL	*Vaccinium*	*elliottii*	Chapman	Mayberry	Shrub	FACW	Ericaceae
VAFU	*Vaccinium*	*fuscatum*	Aiton	Hairy highbush blueberry, black highbush blueberry	Shrub	FACW	Ericaceae
VAMY	*Vaccinium*	*myrsinites*	Lamarck	Southern evergreen blueberry	Subshrub	FACU	Ericaceae
VAST	*Vaccinium*	*stamineum*	Linnaeus	Common deerberry	Shrub	FACU	Ericaceae
VEAN	*Vernonia*	*angustifolia*	Michaux	Carolina sandhill ironweed, carolina slender ironweed	Forb	FACU	Asteraceae
XYCA	*Xyris*	*caroliniana*	Walter	Pineland yellow-eyed-grass	Forb	FACW	Xyridaceae

Table A6. Fire history of Schwalbea populations at Ichauway.

Date/Site	**Jericho**	**Rhexia**	**Parmalee**	**Pond 32**
1992	3/1992	3/1992	3/1992	3/1992
1993	3/1993 (partial), 6/1993 (partial), no burn (partial)	3/1993 (partial), 6/1993 (partial), no burn (partial)	3/1993 (partial), 6/1993 (partial), no burn (partial)	3/1993 (partial), 6/1993 (partial), no burn (partial)
1994	-	3/4/1994 (partial), no burn (partial)	3/4/1994	2/1/1994 (partial), no burn (partial)
1995	dormant season burn not on map, 6/9/1995 (partial), no burn (partial)	3/29/1995 (partial), 6/9/1995 (partial), no burn (partial)	6/9/1995 (partial), no burn (partial)	3/28/1995 (partial), 6/9/1995 (partial), no burn (partial)
1996	-	-	-	-
1997	4/8/1997	4/7/1997	4/14/1997	4/7/1997
1998	-	-	-	-
1999	3/17/1999	5/14/1999	5/28/1999	3/16/1999
2000	-	-	-	-
2001	3/9/2001	3/9/2001	3/23/2001	3/9/2001
2002	-	3/21/2002	-	-
2003	3/12/2003	-	3/13/2003	2/11/2003
2004	-	5/3/2004	-	-
2005	2/7/2005	5/24/2005	5/12/2005	2/4/2005
2006	-	4/24/2006	4/27/2006	3/14/2006
2007	2/15/2007	-	-	-
2008	-	4/14/2008	2/28/2008	2/8/2008
2009	2/17/2009	-	-	6/12/2009
2010	-	1/27/2010	2/26/2010	-
2011	3/2/2011	-	-	7/25/2011
2012	-	6/13/2012	5/22/2012	-
2013	2/21/2013	3/13/2013	3/14/2013	1/31/2013
2014	-	-	-	-
2015	2/20/2015	4/23/2015	3/17/2015	7/1/2015
2016	-	-	-	6/8/2016
2017	2/20/2017	6/27/2017	5/2/2017	7/6/2017
2018	-	6/4/2018	-	6/5/2018
2019	3/8/2019	-	-	6/14/2019
2020	-	5/11/2020	4/16/2020	4/15/2020
2021	4/22/2021	4/22/2021	4/22/2021	6/16/2021
2022	-	4/27/2022	4/27/2022	6/10/2022

Table A7. Species list (Habitat suitability site visits). Species list of species observed at sites during habitat suitability model evaluation.

Species Code	**Genus**	**Species**	**Common Name**	**Authority**
ACRU	Acer	rubrum	Red Maple	L.
AGFA	Agalinis	fasciculata	Beach False Foxglove	(Elliott) Rafinesque
ALAL	Ailanthus	altissima	Tree of Heaven	(Mill.) Swingle
AMAT	Ambrosia	artemisiifolia	Common Ragweed	L.
AN01	Andropogon	sp.		
ANDE	Angelica	dentata	Angelica	(Chapm.) J.M.Coult. & Rose
ANGL	Andropogon	glomeratus	Bushy bluestem	(Walter) Britton, Sterns, & Poggenburg
ANVR	Andropogon	virginicus	Broomsedge Bluestem	L.
ARBE	Aristida	beyrichiana	Wiregrass	Trinius & Ruprecht
ARST	Aristida	stricta	Pineland three-awn grass	Michx.
ARTE	Arundinaria	tecta	Switchcane	(Walter) Muhl.
ASSP	Asimina	spatulata	Slimleaf pawpaw	(Kral) D.B. Ward
BAHA	Baccharis	halimifolia	Sea-myrtle; groundsel tree	L.
BI01	Betula	sp.	Birch sp.	
BICA	Bignonia	capreolata	Crossvine	L.
CAAE	Callicarpa	americana	Beautyberry	L.
CACO	Carya	cordiformis	Bitternut hickory	(Wangenheim) K. Koch
CAGL	Carya	glabra	Pignut hickory	(P. Miller) Sweet
CATO	Carya	tomentosa	Mockernut hickory	(Lamarck) Nuttall
CEAM	Ceanothus	americanus	New Jersey tea	L.
CHLA	Chasmanthium	latifolium	River oats	(Michaux) Yates
CHMA	Chrysopsis	mariana	Maryland golden aster	(L.) Elliott
CHNC	Chamaecrista	nictitans	Sensitive plant	(L.) Moench
CHTH	Chamaecyparis	thyoides	Eastern whitecedar	(L.) Britton, Sterns & Poggenb.
CLAL	Clethra	alnifolia	Pepperbush	L.
COFL	Cornus	floridana	Dogwood	L.
CTAR	Ctenium	aromaticum	Toothache grass	(Walter) Wood
CYRA	Cyrilla	racemiflora	Titi	L.
DEFL	Desmodium	floridanum	Florida tick-trefoil	Chapman
DELI	Desmodium	lineatum	Matted tick-trefoil	A.P. de Candolle
DEMA	Desmodium	marilandicum	Maryland tick-trefoil	(L.) A.P. de Candolle
DEVI	Desmodium	viridiflorum	Velvety tick-trefoil	(L.) A.P. de Candolle
DI02	Dicanthelium	sp.		
DIAG	Dichanthelium	angustifolium	Narrowleaf witchgrass	(Elliott) Gould
DIOV	Dichanthelium	ovale	Oval-flowered witchgrass	(Elliott) Gould & Clark

DISP	Dichanthelium	sphaerocarpon	Round-fruited witchgrass	(Elliott) Gould
DIVR	Diospyros	virginiana	American persimmon	L.
DYOB	Dyschoriste	oblongifolia	Blue twinflower	(Michaux) Kuntze
ELEL	Elephantopus	elatus	Southern elephant's foot	Bertoloni
EPRE	Epigaea	repens	Trailing arbutus	L.
ERAL	Erianthus	alopecuroides	Silver plumegrass	(L.) Elliott
ERPR	Eryngium	prostratum	Blue eryngo	Nuttall ex A.P. de Candolle
ERTO	Eriogonum	tomentosum	Sandhill wild buckwheat	Michaux
EUCA	Eupatorium	capillifolium	Dogfennel	(Lamarck) Small
EUCO	Eupatorium	compositifolium	Coastal dogfennel	Walter
EUGR	Euthamia	graminifolia	Grass-leaved goldenrod	(L.) Nutt.
EUHY	Eupatorium	hyssopifolium	Hyssopleaf Eupatorium	L.
EULE	Eupatorium	leptophyllum	Limesink dogfennel	A.P. de Candolle
EURO	Eupatorium	rotundifolium	Roundleaf eupatorium	L.
GADU	Gaylussacia	dumosa	Southern dwarf huckleberry	(Andrews) Torrey & A. Gray
GAFR	Gaylussacia	frondosa	Blue huckleberry	(L.) Torr. & A.Gray
GAMO	Gaylussacia	mosieri	Woolly huckleberry	Small
GANA	Gaylussacia	nana	Dwarf dangleberry	(A. Gray) Small
GEOB	Geobalanus	oblongifolius	Gopher apple	(Michaux) Small
GESE	Gelsemium	sempervirens	Carolina jessamine	(L.) St. Hilaire
HAVI	Hamamelis	virginiana	Witch-hazel	L.
HEAI	Hexastylis	arifolia	Little brown-jugs	(Michaux) Small
HEAN	Helianthus	angustifolius	Narrowleaf sunflower	L.
HERA	Helianthus	radula	Rayless sunflower	(Pursh) Torrey & A. Gray
HESU	Heterotheca	subaxillaris	Camphorweed	(Lamarck) Britton & Rusby
HYCR	Hypericum	crux-andreae	St. Peter's wort	(L.) Crantz
HYHY	Hypericum	hypericoides	St. Andrew's Cross	(L.) Crantz
ILCO	Ilex	coriaceae	Large gallberry	(Pursh) Chapm.
ILGL	Ilex	glabra	Inkberry	(L.) A. Gray
ILMY	Ilex	myrtifolia	Myrtle holly	Walter
ILOP	Ilex	opaca	American holly	Aiton
ILVO	Ilex	vomitoria	Yaupon holly	Aiton
IOLI	Ionactis	linariifolia	Stiff-leaved aster	(L.) Greene
LA01	Lachnocaulon	sp.	Bogbutton	
LE01	Lechea	sp		
LI01	Liatris	sp.	Blazing star	
LILU	Ligustrum	lucidum	Glossy privet	W.T.Aiton
LISI	Ligustrum	sinense	Chinese privet	Loureiro
LIST	Liquidambar	styraciflua	Sweetgum	L.

LITU	Liriodendron	tulipifera	Tulip tree	L.
LOJA	Lonicera	japonica	Japanese honeysuckle	Thunberg
LS01	Lespedeza	sp.		
LS02	Lespedeza	spp.		
LU01	Ludwigia	sp.		
LYLI	Lyonia	ligustrina	He-huckleberry	(L.) DC.
LYLU	Lyonia	lucida	Shining fetterbush	(Lamarck) K. Koch
LYMA	Lyonia	mariana	Staggerbush	(L.) D.Don
MAGR	Magnolia	grandiflora	Southern magnolia	L.
MAVI	Magnolia	virginiana	Sweetbay	L.
MIRE	Mitchella	repens	Partridgeberry	L.
MOCE	Morella	cerifera	Wax-myrtle	(L.) Small
MOPU	Morella	pumila	Dwarf wax-myrtle	(Michx.) Small
MU01	Muhlenbergia	sp.	Muhly	
MURO	Muscadinia	rotundifolia	Muscadine	(Michaux) Small
NEAR	Nekemias	arborea	Peppervine	(L.) J. Wen & Boggan
NYSY	Nyssa	sylvatica	Blackgum	Marshall
OSCI	Osmundastrum	cinnamomeum	Cinnamon fern	(L.) C. Presl
OXAR	Oxydendrum	arboreum	Sourgum	(L.) DC.
PAQU	Parthenocissus	quinquefolia	Virginia creeper	(L.) Planchon
PEPA	Persea	palustris	Swamp bay	(Rafinesque) Sargent
PIAA	Pityopsis	aspera	Silver grass	(Shuttleworth ex Small) Small (Fernald) Semple & F.D. Bowers
PIEL	Pinus	elliottii	Slash pine	Engelmann
PIGR	Pityopsis	graminifolia	Grass-leaved goldenaster	(Michaux) Nuttall
PIPA	Pinus	palustris	Longleaf pine	P. Miller
PISE	Pinus	serotina	Pond pine	Michx.
PITA	Pinus	taeda	Loblolly pine	L.
PRSE	Prunus	serotina	Black cherry	Ehrhart
PTPS	Pteridium	pseudocaudatum	Southern bracken fern	(Clute) Christenhusz
PTPY	Pterocaulon	pycnostachyum	Blackroot	(Michaux) Elliott
QUAL	Quercus	alba	White oak	L.
QUBI	Quercus	bicolor	Swamp chestnut oak	Willd.
QUEL	Quercus	elliottii	Running oak	Wilbur
QUFA	Quercus	falcata	Southern red oak	Michaux
QUGE	Quercus	geminata	Sand live oak	Small
QUHE	Quercus	hemisphaerica	Sand laurel oak	Bartram ex Willdenow
QUIN	Quercus	incana	Bluejack oak	Bartram
QULA	Quercus	laurifolia	Laurel oak	Michaux
QUMA	Quercus	marilandica	Blackjack oak	Ashe ex Small
QUMI	Quercus	michauxii	Basket oak	Nuttall
QUNI	Quercus	nigra	Water oak	L.
QUPH	Quercus	phellos	Willow oak	L.

QUVI	Quercus	virginiana	Live oak	P. Miller
RD01	Rhododendron	sp.	Unknown rhododenron (not flowering)	
RHAL	Rhexia	alifanus	Smooth meadow-beauty	Walter
RHCO	Rhus	copallinum	Winged sumac	L.
RHMA	Rhexia	mariana	Meadow-beauty	Michaux
RHRE	Rhynchosia	reniformis	Dollarweed	A.P. de Candolle
ROHI	Robinia	hispida	Bristly locust	L.
RUCU	Rubus	cuneifolius	Sand blackberry	Pursh
SAAL	Sassafras	albidum	Sassafras	(Nuttall) Nees
SAFL	Sarracenia	flava	Yellow pitcher plant	L.
SAGI	Saccharum	gigantea	Sugarcane plumegrass	(Walter) Pers.
SAMI	Sabal	minor	Dwarf palmetto	(Jacquin) Persoon
SCTE	Schizachyrium	tenerum	Slender bluestem	Nees
SECA	Seymeria	cassioides	Yaupon black senna	(J.F. Gmelin) Blake
SELI	Sericocarpus	linifolius	Narrowleaf whitetop aster	Britton, Sterns & Poggenb.
SMAU	Smilax	auriculata	Dune greenbriar	Walter
SMBO	Smilax	bona-nox	Catbriar	L.
SMRO	Smilax	rotundifolia	Common greenbriar	L.
SOAP	Solidago	altissima	Oldfield goldenrod	L. M.C. Johnston
SONU	Sorghastrum	nutans	Yellow Indiangrass	(L.) Nash
SOOD	Solidago	odora	Licorice goldenrod	Aiton
SOTO	Solidago	tortifolia	Leafy pineywoods goldenrod	Elliott
SPJU	Sporobolus	junceus	Pineywoods dropseed	(Palisot de Beauvois) Kunth
SY01	Symphyotrichum	sp.	Aster	
SYCO	Symphyotrichum	concolor	Eastern silveryaster	(L.) Nesom
SYTI	Symplocos	tinctoria	Sweetleaf	(L.) L'Héritier
SYWA	Symphyotrichum	walteri	Walter's aster	(Alexander) G.L.Nesom
TAAS	Taxodium	ascendens	Pond cypress	Brongniart
TADI	Taxodium	distichum	Bald cypress	(L.) L.C. Richard
TEVI	Tephrosia	virginiana	Virginia goats-rue	(L.) Persoon
TIAM	Tilia	americana	Southern basswood	L. (P. Miller) Castiglioni
TOPU	Toxicodendron	pubescens	Poison oak	P. Miller
TORA	Toxicodendron	radicans	Poison ivy	(L.) Kuntze
TOVE	Toxicodendron	vernix	Poison sumac	(L.) Kuntze
TRDI	Trichostema	dichotomum	Bluecurls	L.
TROD	Trilisa	odoratissima	Vanilla-leaf	(J.F. Gmelin) Cassini
TRSM	Tragia	smallii	Gulf-coast noseburn	Shinners
TRUR	Tragia	urens	Sandhill noseburn	L.
UNK GRASS				
UNK. LEGUME				
VAAR	Vaccinium	arboreum	Farkleberry	Marshall

VACR	Vaccinium	crassifolium	Creeping blueberry	Andrews
VAEL	Vaccinium	elliottii	Mayberry	Chapman
VAFU	Vaccinium	fuscatum	Hairy highbush blueberry	Aiton
VAMY	Vaccinium	myrsinites	Southern evergreen blueberry	Lamarck
VAST	Vaccinium	stamineum	Deerberry	L.
VEAN	Vernonia	angustifolia	Ironweed	Michaux
XY01	Xyris	sp.		