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Research Article

Microsite Habitat, Species Associations, and Habitat Suitability Model of a Globally Imperiled Shrub

Clayton W. Hale,[1] Joshua J. Granger,[1,4] Courtney M. Siegert,[1] Sandra B. Correa,[2] Janice L. DuBien,[3] Caleb D. Goldsmith,[1] and Will Kruckeberg[1]

[1]Department of Forestry, Mississippi State University, Mississippi State, MS 39762
[2]Department of Wildlife, Fisheries and Aquaculture, Mississippi State University, Mississippi State, MS 39762
[3]Department of Mathematics and Statistics, Mississippi State University, Mississippi State, MS 39762

[4]Corresponding author: joshua.j.granger@msstate.edu

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ABSTRACT

Miller's witch-alder (*Fothergilla milleri*, Hamamelidaceae) is a newly described globally imperiled shrub that is known from disjunct populations in coastal Alabama, the panhandle of Florida, and one location in Georgia. Little is currently known about the natural history or ecology of the species. We conducted inventories of three populations of *F. milleri* in Alabama and Florida. A total of 3060 ramets were found; 45% were in one subpopulation $\leq$0.5 ha in area and 79% were in one population within an area of 4.5 ha. Low ramet counts in few locations makes the species particularly vulnerable to extinction due to stochastic events. Also, all seed capsules found within the surveys were infected by an aphid, which is possibly preventing sexual reproduction within the populations. Microsite habitat data indicated *F. milleri* grows in a unique transitional habitat between upland conifer forest and wetlands. The sites where extant populations of *F. milleri* inhabit tend to have acidic and well-drained soils with a high sand content. Further, many populations were under thick midstory vegetation. Thus, fire or other forms of removal may be needed to release those subpopulations before they may become shaded out. Lastly, a habitat suitability model was developed to better facilitate conservation efforts. However, only 0.5% of the study area was within the highest level of suitability. *Fothergilla milleri* is facing multiple threats that could lead to its extirpation from the wild, and direct and intense conservation action may be necessary to ensure *F. milleri* remains on the landscape.

Index terms: Hamamelidaceae; Maxent; microsite; Miller's witch-alder; plant conservation

INTRODUCTION

Miller's witch-alder (*Fothergilla milleri* W.D. Phillips & J.E. Haynes; Hamamelidaceae) is a small shrub endemic to the Gulf Coast Plain of Alabama, the panhandle of Florida, and one county in Georgia (Haynes et al. 2020; Figure 1). *Fothergilla milleri* is most similar morphologically to dwarf witch-alder (*Fothergilla gardenii* L.) and was not identified as a unique species until 2020 (Haynes et al. 2020). The largest morphological differences between these two species are the orientation of the leaves; *F. milleri* leaves tend to be held erect, while *F. gardenii* leaves tend to be spreading (Haynes et al. 2020). Additionally, *F. milleri* varies genetically from *F. gardenii*. *Fothergilla milleri* presents diploid chromosomes while *F. gardenii* presents tetraploid chromosomes (Haynes et al. 2020). According to genetic research conducted by Haynes et al. (2020), the only other diploid species in the genus is *F. parvifolia* (Kearney). *Fothergilla parvifolia* and *F. milleri* differ by geographical distribution with *F. parvifolia* occurring primarily in eastern Georgia and South Carolina and by morphological differences with *F. parvifolia* tending to have leaves that droop along the stems (Haynes et al. 2020). Beyond morphological descriptions and brief habitat generalizations included in the species description (Haynes et al. 2020), little is known about the newly described *F. milleri*. This large knowledge gap in the ecology, habitat needs, and current conservation status severely limits conservationists' ability to protect and manage for the species.

Fothergilla milleri has been ranked as a G2 globally imperiled species by NatureServe (NatureServe Explorer 2021). The lack of naturally occurring fire regimes have been considered one factor leading to the decline of *F. gardenii* populations across their natural range (Barger et al. 2013; Haynes et al. 2020). Due to similarities in habitat and distribution, fire suppression is likely a factor impacting *F. milleri* abundance as well. Although no study known to the authors has quantified the effects of fire on *F. milleri* populations, it is thought the species requires the fire disturbance to create gaps in the canopy and increase sunlight to the forest floor. With so few known populations, another threat currently facing *F. milleri* is environmental stochasticity. For example, while moderate disturbance may support regeneration of *F. milleri*, one extreme environmental event, such as a severe fire or tropical cyclone, could potentially reduce or eliminate extant populations of *F. milleri* (Menges 1992). Other examples of environmental stochasticity include extended droughts, late spring frosts that damage new growth and flowers, or tornados.

Modeling the habitat suitability of rare and imperiled plant species has become an integral part of plant conservation (Kumar and Stohlgren 2009; Yang et al. 2013; Remya et al. 2015; Sharma et al. 2018; Ramirez-Reyes 2021). Habitat suitability models allow plant conservationists to more effectively allocate resources to areas that are more likely to support the species of concern. Additionally, habitat suitability models can concentrate

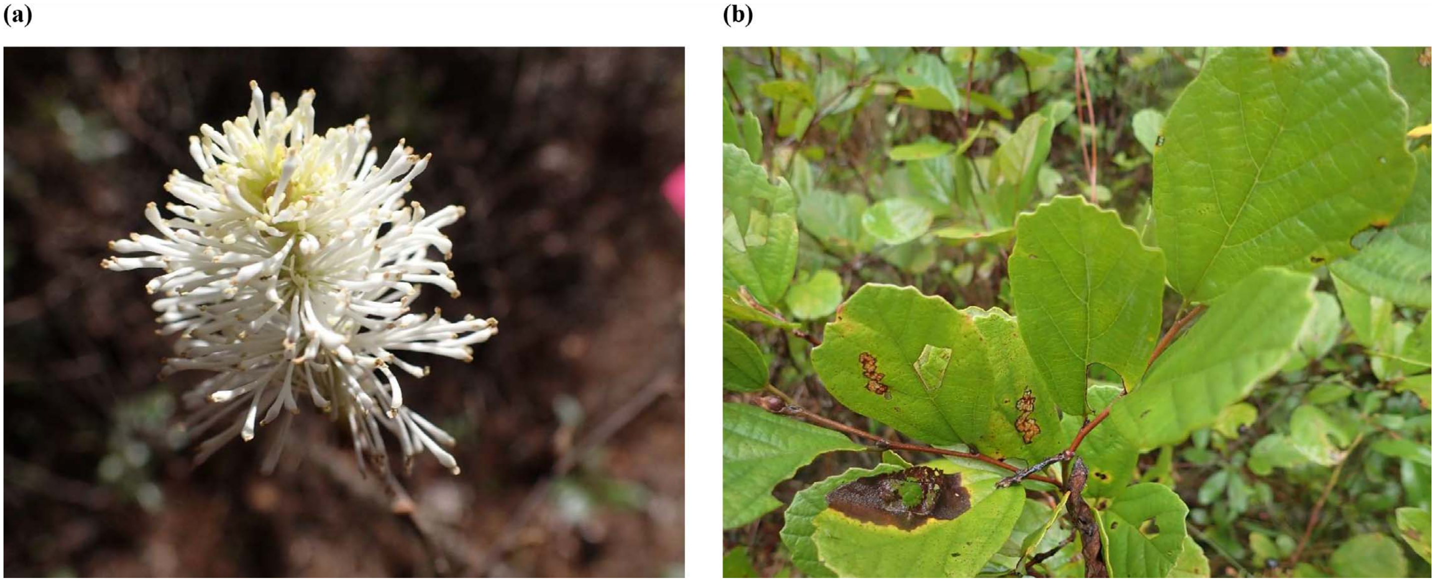

Figure 1.—(a) Typical reproductive morphology of *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae). (b) Typical vegetative morphology of *Fothergilla milleri*. Photos taken by the authors.

survey efforts on habitats that are most likely to support the species (Costa et al. 2010). Several methodologies are available to produce habitat suitability models; however, one of the more popular methods is maximum entropy, or Maxent (Philips et al. 2006). Maxent seems to perform particularly well for species with small sample sizes, like that of *F. milleri*, due to the robustness of the model (Hernandez et al. 2006; Wisz et al. 2008). Habitat suitability models can therefore aid conservation activities to help ensure the perpetuation of rare and imperiled plant species on the landscape (Hemati et al. 2020).

The main objectives of this study were to (1) assess the conservation status of the three largest known populations of *F. milleri*, (2) quantify the microhabitats and species associations where *F. milleri* occurs, and (3) provide a preliminary habitat suitability map to assist conservationists with future decision making. The last two objectives were designed to facilitate the identification of suitable areas for *F. milleri* establishment. Results of this model open the possibility of out planting, or introducing, *F. milleri* into areas with high habitat suitability. *Fothergilla milleri* is not currently widely available in the nursery trade, however *F. gardenii* is (Ranney et al. 2007). Understanding the habitat needs of *F. milleri* in the wild, particularly soil conditions and optimal light conditions, may facilitate horticulturalists in bringing *F. milleri* into cultivation.

METHODS

Sampling Areas

Through personal communication with the species expert, Dr. Ron Miller, we identified the three largest known populations of *F. milleri* (Figure 2). One smaller population of *F. milleri* was known; however, it was not used due to a lack of access and small population size. The first population inventoried is within the Perdido Wildlife Management Area, approximately 5 km east of Gateswood in Baldwin County, Alabama, USA. The second population is approximately 2 km west of the city of Geneva in Geneva County, Alabama, USA. The third population is located approximately 10 km northeast of the city of Crestview in Okaloosa County, Florida, USA. Hereinafter, these populations will be referred to by the county in which they are located (Baldwin County, Geneva County, and Okaloosa County). *Fothergilla milleri* grew in well-defined patches within the Baldwin and Okaloosa populations; each of these patches was therefore defined as a subpopulation within the main population. In total, nine subpopulations were defined in the Baldwin population, five in the Okaloosa population, and one in the Geneva population.

Ramet Counts and Seed Capsule Assessment

A 100% inventory of *F. milleri* was conducted in all populations, except one subpopulation in Okaloosa County that was subjected to a prescribed burn before a 100% survey could be conducted. A preliminary survey using a modified point-centered quarter, or Wisconsin plot, method was conducted before the prescribed burn; therefore, for this one subpopulation, an estimated number of *F. milleri* ramets was used (Cottam and Curtis 1956). For this one subpopulation within the Okaloosa population, a 20 m transect was established through the population. Three points, one at either end and one in the middle, were then established. At each point, four 0.25 m^2 quadrats were placed at a random distance 1–5 m away from the point at 45°, 135°, 225°, and 315° offsets from the transect. All *F. milleri* ramets were counted within the quadrat then summed for each of the four points. The results of the transect were then extrapolated to the total size of the subpopulation. For all other subpopulations within the Baldwin, Geneva, and Okaloosa populations a 100% systematic survey was carried out. Due to the rhizome growth form of *F. milleri* differentiating between genetic individuals (or genets) would be difficult to nearly impossible without extensive genetic analysis of each ramet. Therefore, ramets (or stems) were counted regardless of if they were genetic individuals or not. A ramet was defined at the soil

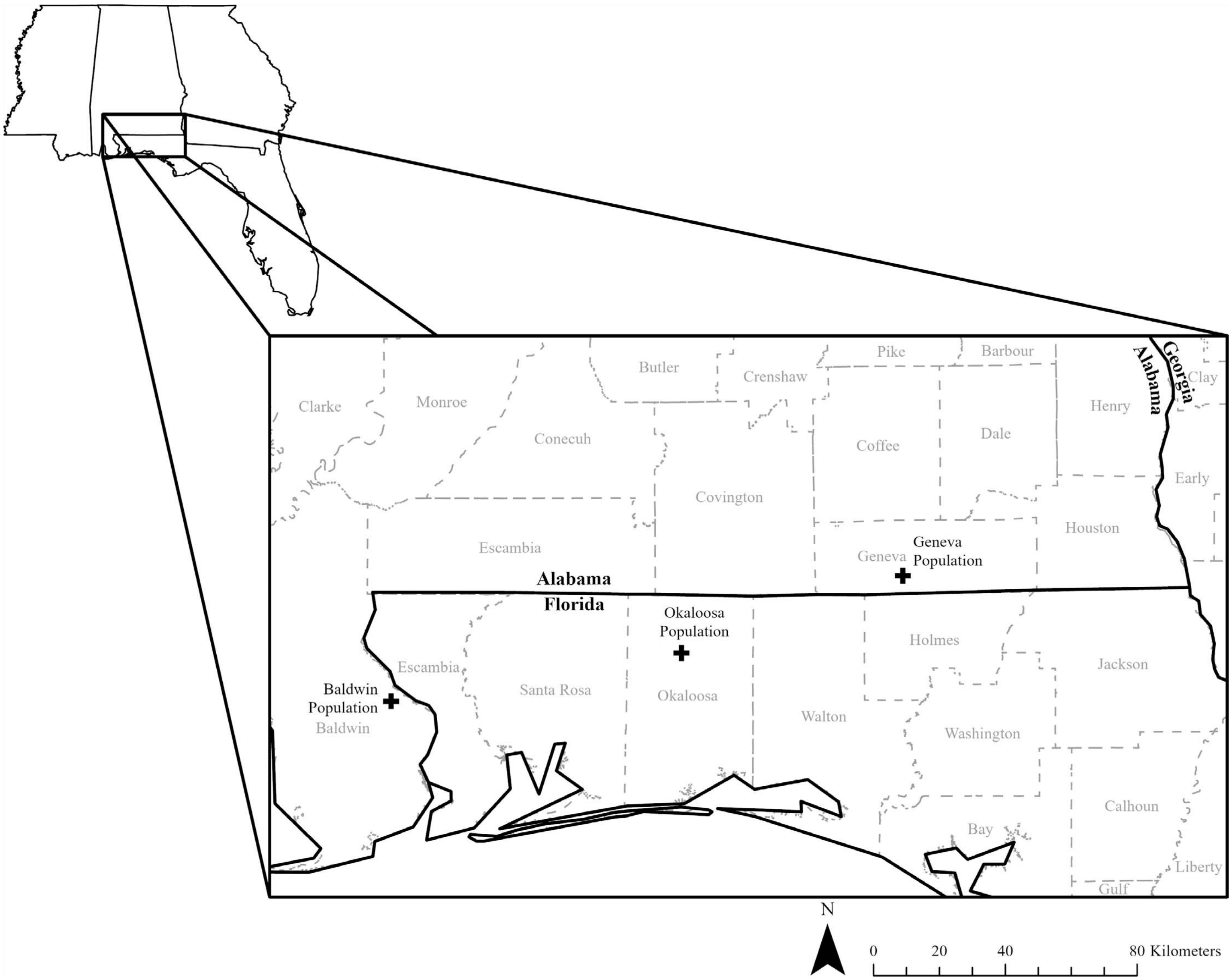

Figure 2.—The location of the three populations of *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae) sampled. These populations were determined to be the largest through personal communication with local species expert, Dr. Ron Miller of Pensacola, Florida.

surface where *F. milleri* was growing from a single point. Lastly, the number of seed capsules that appeared healthy and uninfected was noted throughout the survey period. In appearance, a viable fruit of *F. milleri* is a loculicidal, ovoid, densely pubescent, capsule (Figure 3a). When fruit capsules become infected by an aphid, they present with no discernable seed capsules and instead present as a hollow chambered gall (Figure 3b). The Geneva and Okaloosa County surveys were conducted in October of 2020, while the Baldwin County survey was conducted in March of 2021.

Woody Vegetation Sampling

Within the Baldwin and Okaloosa County populations, the distribution of *F. milleri* was patchy and noncontiguous. To assess species associations, for each subpopulation of *F. milleri* located within each population, a woody vegetation sampling plot was established in the center of the subpopulation. In total, nine woody vegetation sampling plots were established within Baldwin County and five within Okaloosa County. The population in Geneva County was a single ~30 m long subpopulation along Goat Hill Road. Two woody vegetation sampling plots were established there, one at either end of the population along the road. Woody vegetation sampling occurred in the Geneva and Okaloosa County populations in October of 2020, and in the Baldwin County population in July of 2020. Overstory species association was determined in fixed-area plots 0.05 ha in size (Figure 4). All woody stems greater than 10 cm diameter at breast height (dbh; 1.4 m) were identified to the species level and dbh was measured. Midstory species association plots were 0.025 ha and were nested within each overstory plot. All woody stems of 2.5–10 cm dbh were identified to the species level. Two diameter measurements were taken at breast height 90° offset of one another using handheld calipers for each stem

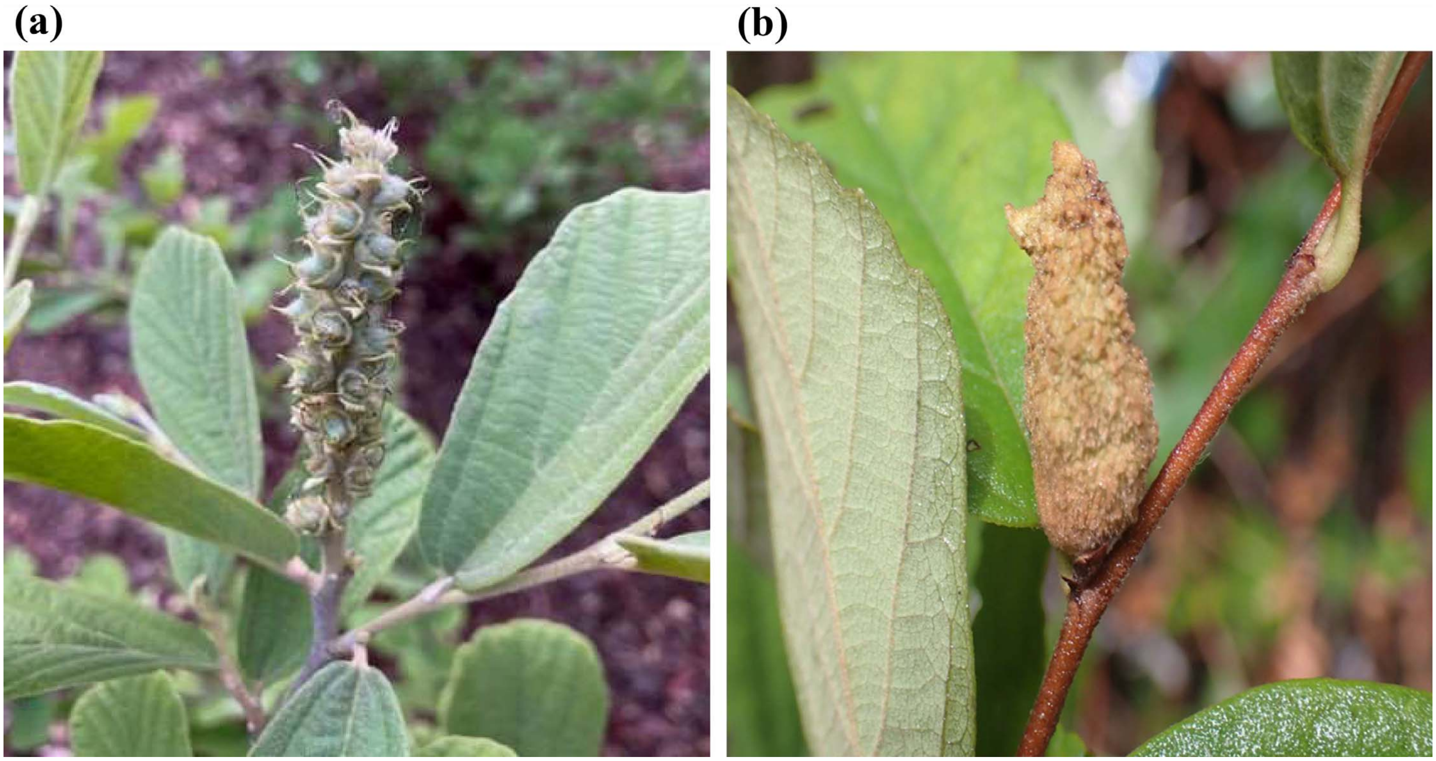

Figure 3.—(a) The seed capsules of a healthy *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae). (b) An infected seed capsule of *F. milleri* by an aphid, likely *Hamamelistes blackmani* (Dederich & von Dohlen). Photos taken by the authors.

within the midstory plots; the two measurements were then averaged for each stem dbh. Two measurements were taken to account for any variation or imperfections (i.e., elongation or imperfect circles) in the circumference of the stem (West 2015).

To determine maximum overstory tree height, the three tallest canopy stems per plot were measured with a clinometer (Suunto Clinometer or TruPulse 200 laser). The three tree heights were then averaged to estimate the average overstory tree height for

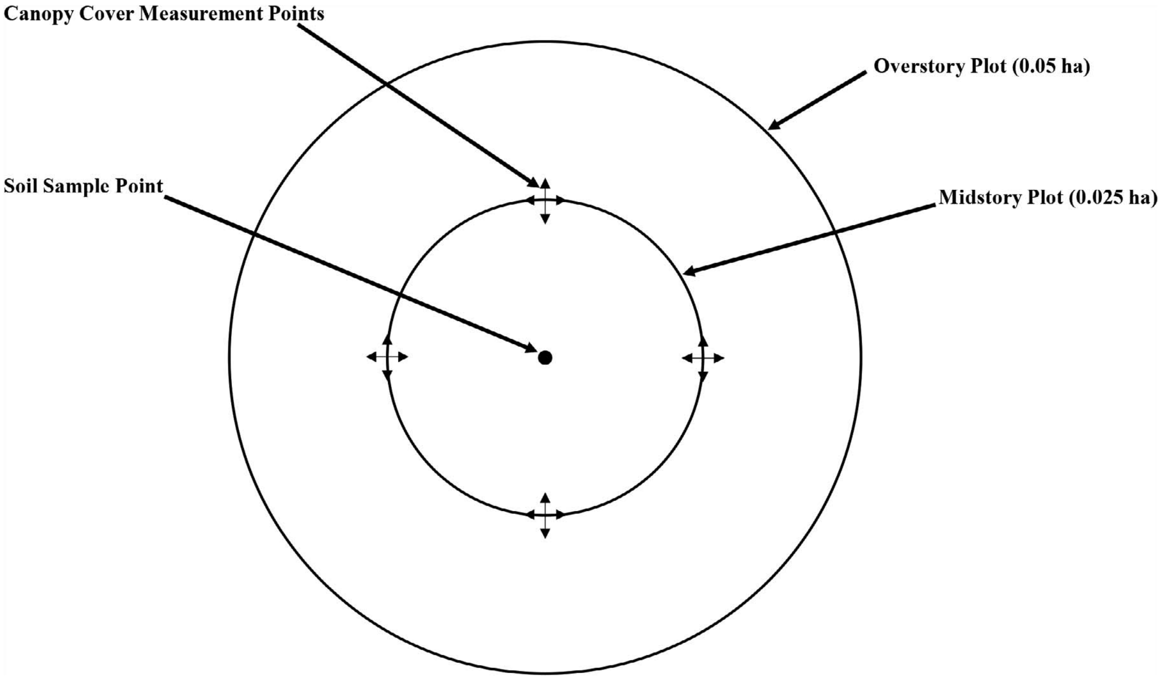

Figure 4.—Plot layout for sampling overstory stems, midstory stems, canopy cover, and soil of the three sampled *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae) populations. Arrows indicate directionality of canopy cover measurement.

each plot. A densiometer (Forest Densiometers Model-c spherical concave) was used to estimate canopy cover. Four canopy cover measurements were taken at each of the four cardinal directions along the perimeter of the midstory vegetation plots. This resulted in a total of 16 canopy cover measurements per plot. These measurements were then averaged to produce one average canopy cover estimate per plot.

A one-way ANOVA was used to assess differences among the three populations in overstory stems/ha, midstory stems/ha, overstory basal area (m^2/ha), midstory basal area (m^2/ha), overstory height (m), and percent canopy cover. If statistical differences were detected, it could indicate differing ecological niches among populations. Both midstory stems/ha and midstory basal area were not normally distributed. Therefore, a square root transformation was conducted to meet the normal distribution assumption of ANOVA. If statistically significant differences were detected among populations a Tukey's pair-wise comparison was then used to determine which populations were different from one another. Additionally, both a Pearson correlation test and simple linear regression models were used to test for a correlation between the number of *F. milleri* ramets and the previously listed woody plant metrics. All tests were conducted with the statistical software R (R Core Team 2020). All results are presented with mean ± the standard error.

Soil Sampling

Soil samples were taken at each of the vegetation plots at the plot center. A 30-cm long soil push probe with a 2 cm diameter was used to collect each soil sample. The sample was divided into two subsamples, the top 0–10 cm of soil and the remaining bottom 10–30 cm. Samples were then placed in resealable plastic bags and placed on ice and later transferred to refrigeration. Soil texture for each sample was determined by feel and by the U.S. Natural Resource Conservation Science Web Soil Survey (Thien 1979; Soil Survey Staff 2021). Soil pH was measured in a 2:1 slurry ratio (HANNA HI 5521 Research Grade pH/EC meter). Upon return to the lab, samples were ground, sieved, and dried at 105 °C prior to analysis. Samples were analyzed for total C, total N, and C:N ratio using elemental combustion (ECS 4010 CHNO-S, Costech, Inc.). Distance to wetlands was assessed from the National Wetlands Inventory (U.S. Fish and Wildlife Service 2020). Soil sampling occurred in the Geneva and Okaloosa County populations in October of 2020, and in the Baldwin County population in July of 2020.

A one-way ANOVA was used to test for differences among the three populations in soil pH and C:N ratio, followed by Tukey's pair-wise post hoc comparisons. Soil C:N ratio was log transformed to meet the normal distribution assumption. Additionally, both a Pearson correlation test and simple linear regression models were used to test for a correlation between the number of *F. milleri* ramets and soil pH, soil horizon depths, and C:N ratios. All tests were conducted with the statistical software R (R Core Team 2020). All results are presented with mean ± the standard error.

Habitat Suitability Model (HSM)

A preliminary habitat suitability model for *F. milleri* was conducted in Maxent 3.4.0 (Phillips et al. 2006). HSMs utilize occurrence records of a species and environmental raster layers to estimate suitable habitat for that species across a defined area. Unlike other HSM methodologies, Maxent utilizes presence-only occurrence data rather than presence–absence data (Phillips et al. 2006; Phillips and Dudík 2008). Opportunistic botanical surveys can therefore be used in the modeling process, as opposed to formal systematic surveys. The study area for the presented model was an ellipse that encompasses all the occurrences used in the modeling process. An ellipse was used around the known occurrences to prevent the model from extrapolating beyond the known boundaries of the species' range. The defined study area was set to encompass approximately 114,115 km^2.

To optimize the presented model, the methodologies of Shcheglovitova and Anderson (2013) were followed. Shcheglovitova and Anderson (2013) combined the methodologies of Anderson and Gonzalez (2011) and Syfert et al. (2013) to optimize both the regularization multiplier and feature class in a combination of one another for use within the final model. These methodologies are designed specifically for modeling applications when there are less than 25 available occurrence points. Various regularization multipliers, as defined by Shcheglovitova and Anderson (2013), were used in combination with various feature classes, or combinations of feature classes. Regularization, or beta, multipliers of 0.5, 0.75, 1.0, 1.25, 1.5, 1.75, and 2 were used in model optimization. The feature classes and feature class combinations used were linear (L), hinge (H), linear with quadratic (LQ), and linear with quadratic and hinge (LQH). With the six regularization multipliers and four feature classes, a total of 28 models were developed. A jackknife, or leave one out, approach was used for each model. The lowest presence threshold rule, or minimum training presence threshold in Maxent, was used to calculate the binary omission rate (Pearson et al. 2007; Shcheglovitova and Anderson 2013) and the optimal model was selected based on the lowest omission rate. Through this process the combination of a regularization multiplier of 1.0 and the linear feature class was found to be optimal and was therefore used in the final model. Background data, or pseudo-absences, were limited to hydrological unit code (HUC) 8 level watersheds that contain one of the eight *F. milleri* occurrences used within the model (U.S. Geological Survey 2010). A uniform prior was therefore assumed within the watersheds (Merow et al 2013). After the modeling process within the watersheds, the model was then projected out to the ellipse study area. In total 5000 background points were used, with all other settings within the Maxent software set on default. Lastly, a jackknife test was used to determine the importance (% contribution) of the various environmental predictor levels within the final model.

GPS coordinates for the occurrences were provided by species expert Dr. Ron Miller. To avoid autocorrelation, occurrence data were rarified to 2 km^2, which was the original size of the largest raster cells. The rarefication tool within the SDMtoolbox was used to accomplish the rarefication (Brown et al. 2017). Sixty-eight occurrences were excluded due to the spatial rarefication process. After the rarefication process, eight occurrences were used in the final model.

Twenty of the 22 originally considered environmental predictor variables were used in the final model. ArcGIS Pro

Table 1.—Relative contribution to of the 20 environmental variables used in developing the preliminary habitat suitability model for *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae).

Environmental variable	Contribution (%)
Mean temperature of warmest quarter (bio10)	30.8
Percent soil sand content	27.5
Precipitation in warmest quarter (bio18)	20.8
Distance to water	11.3
Isothermality (bio3)	6.7
Mean temperature of coldest quarter (bio11)	1.3
Annual mean temperature (bio1)	0.8
Soil pH	0.5
Precipitation seasonality (bio15)	0.2
Max. temperature of warmest month (bio5)	0.0
Precipitation of wettest quarter (bio16)	0.0
Precipitation of driest quarter (bio17)	0.0
Precipitation of driest month (bio14)	0.0
Precipitation of wettest month (bio13)	0.0
Annual precipitation (bio12)	0.0
Mean diurnal range (bio2)	0.0
Precipitation of coldest quarter (bio19)	0.0
Temperature seasonality (bio4)	0.0
Min. temperature of coldest month (bio6)	0.0
Temperature annual range (bio7)	0.0

2.4.3 was used to prepare all environmental layers (Table 1). Similar to the methodologies of Shcheglovitova and Anderson (2013), we initially used 19 bioclimatic variables within the WorldClim dataset (Fick and Hijmans 2017). The 19 bioclimatic variables considered were annual mean temperature (bio1), mean diurnal range (bio2), isothermality (bio3), temperature seasonality (bio4), maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), temperature annual range (bio7), mean temperature of the wettest quarter (bio8), mean temperature of the driest quarter (bio9), mean temperature in the warmest quarter (bio10), mean temperature of the coldest quarter (bio11), annual precipitation (bio12), precipitation in the wettest month (bio13), precipitation in the driest month (bio14), precipitation seasonality (bio 15), precipitation of the wettest quarter (bio16), precipitation of the driest quarter (bio17), precipitation of the warmest quarter (bio18), and precipitation of the coldest quarter (bio19). However, the mean temperature of the wettest quarter (bio8) and the mean temperature of the driest quarter (bio9) were dropped from the final model. Their inclusion in the final model produced bands within the map that were inappropriate at the scale of this model. These bioclimatic datasets are biologically relevant climatic data indices that are calculated using standard climate data from 1970 to 2000 (Fick and Hijmans 2017). Worldclim's bioclimatic data has been used successfully to model other rare plant species (Yang et al. 2013; Abdelaal et al. 2019; Ramirez-Reyes et al. 2021). The 30 second, or ca. 1 km^2, resolution was used for all WorldClim environmental predictor layers. In addition to the 17 bioclimatic datasets used in the final model, three other environmental predictor variables were developed and used within the final model. Due to anecdotal evidence of *F. milleri* growing near wetlands reported by conservationists, the Euclidean distance from a body of water was estimated. To create this layer, the USA Detailed Streams layer was rasterized and used within the Euclidean distance function in ArcGIS Pro (Gary et al. 2009). The two remaining environmental predictor layers were soil pH and percent sand content; both were downloaded from the SSURGO database at 30 m resolution (Soil Survey Staff 2019).

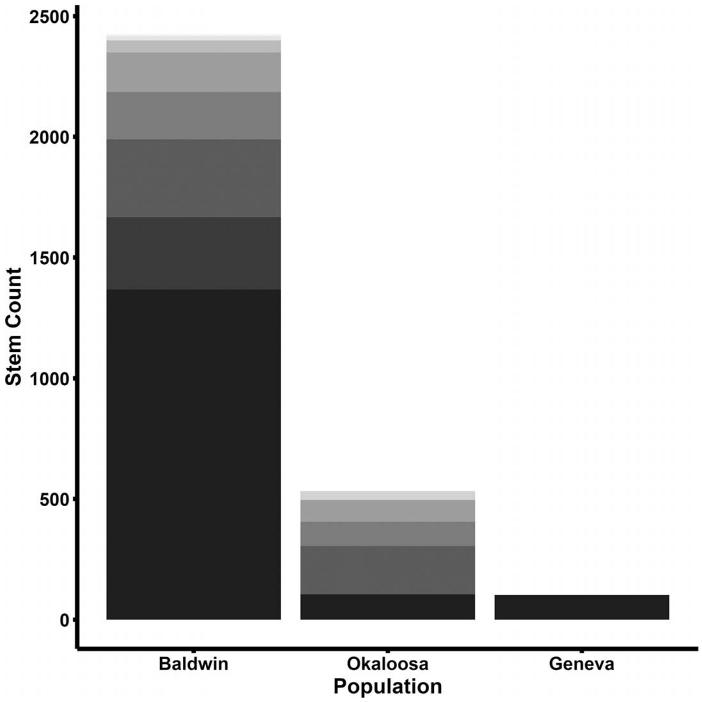

Figure 5.—Ramet counts of *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae) for each of the three populations sampled. Shading indicates different *F. milleri* subpopulations within each population.

After the final model was developed, the map produced by Maxent was further analyzed. Each pixel within the habitat suitability map was binned into discrete classes for each tenth of habitat suitability. The 0.9–1 habitat suitability bin is considered to represent habitat that would be of the highest suitability for the species.

RESULTS

Ramet Counts and Seed Capsule Assessment

A total of 3060 *F. milleri* ramets were counted across all three populations (Figure 5). The Baldwin County population contained the largest number of ramets (2425 ramets) followed by the Okaloosa County population (503 ramets) and the Geneva County population (102 ramets). The one subpopulation within the Okaloosa County population of *F. milleri* that could not be fully counted due to the prescribed burn had an estimated 200 ± 116 ramets. One subpopulation of *F. milleri* within the Baldwin population accounted for 1367 ramets, or 45% of all ramets counted across the populations. Lastly, all seed capsules found throughout the inventories were found to be infected by an aphid species. This aphid is likely the newly described *Hamamelistes blackmani* (Dederich et al. 2022).

Table 2.—Average stems/ha and basal area/ha of associated woody plant species within the three sampled populations of *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae). Standard errors are presented parenthetically.

Species	Stems/ha	Basal area/ha (m^2)
Overstory		
Pinus taeda	161 (57)	5.9 (2.0)
Pinus palustris	80 (36)	4.5 (2.1)
Chamaecyparis thyoides	79 (41)	2.4 (1.2)
Cliftonia monophylla	48 (20)	0.6 (0.3)
Pinus elliottii	41 (19)	3.0 (1.2)
Magnolia virginiana	19 (9)	0.4 (0.1)
Liriodendron tulipifera	11 (6)	0.4 (0.2)
Quercus nigra	11 (5)	0.5 (0.3)
Quercus virginiana	9 (8)	0.3 (0.3)
Nyssa sylvatica	8 (4)	0.3 (0.2)
Quercus phellos	6 (4)	0.1 (0.1)
Ilex opaca	4 (3)	0.1 (0.0)
Taxodium distichum	4 (3)	0.2 (0.2)
Acer rubrum	3 (3)	0.0 (0.0)
Cyrilla racemiflora	1 (1)	0.0 (0.0)
Midstory		
Cliftonia monophylla	213 (88)	0.5 (0.3)
Ilex coriacea	101 (64)	0.1 (0.1)
Magnolia virginiana	64 (28)	0.1 (0.0)
Chamaecyparis thyoides	43 (23)	0.2 (0.1)
Cyrilla racemiflora	37 (27)	0.0 (0.0)
Acer rubrum	27 (11)	0.1 (0.0)
Nyssa sylvatica	24 (10)	0.1 (0.0)
Pinus taeda	24 (15)	0.1 (0.1)
Quercus nigra	13 (5)	0.0 (0.0)
Quercus phellos	13 (13)	0.0 (0.0)
Liriodendron tulipifera	5 (5)	0.0 (0.0)
Myrica cerifera	5 (5)	0.0 (0.0)
Pinus palustris	5 (5)	0.0 (0.0)
Taxodium distichum	5 (4)	0.0 (0.0)
Ilex vomitoria	3 (3)	0.0 (0.0)

Woody Vegetation Structure

Mean overstory stems per hectare across all woody vegetation sampling plots was 484 ± 218 stems/ha. The most common species within the overstory plots containing *F. milleri* were loblolly pine (*Pinus taeda* L.), representing 33.3% of overstory stems (161 ± 57 stems/ha; Table 2). The second and third most common species were longleaf pine (*Pinus palustris* Mill.) and Atlantic white-cedar (*Chamaecyparis thyoides* (L.) Britton, Sterns & Poggenb.) (80 ± 36 stems/ha and 79 ± 41 stems/ha, respectively). Mean basal area within the overstory vegetation plots was 18.4 ± 8.1 m^2/ha. The species with the highest mean basal area per hectare was loblolly pine (5.9 ± 2.0 m^2/ha), followed by longleaf pine and slash pine (*Pinus elliottii* Engelm.) (4.5 ± 2.1 m^2/ha and 3.0 ± 1.2 m^2/ha, respectively). No statistically significant differences were detected between populations with respect to either overstory stems/ha (*F* value = 1.253, $P = 0.318$) or basal area (*F* value = 1.131, $P = 0.352$). See Supplemental Appendix for ANOVA statistic tables and Tukey's pairwise comparison results.

Mean midstory stems per hectare across all woody vegetation sampling plots was 584 ± 307 stems/ha (± SE; Table 2). The most common species within midstory vegetation plots was buckwheat tree (*Cliftonia monophylla* (Lam.) Britton ex Sarg) (213 ± 88 stems/ha), followed by large gallberry (*Ilex coriacea* (Pursh) Chapm) and sweetbay magnolia (*Magnolia virginiana* L.) (101 ± 65 stems/ha and 64 ± 29 stems/ha, respectively). Mean basal area within the midstory was 1.2 ± 0.7 m^2/ha. The species with the highest basal area was buckwheat tree (0.5 ± 0.3 m^2/ha), followed by Atlantic white-cedar and large gallberry (0.2 ± 0.1 m^2/ha and 0.1 ± 0.1 m^2/ha, respectively). Both midstory stems/ha (*F* value = 11.34, $P = 0.001$) and midstory basal area (*F* value = 6.266, $P = 0.012$) varied significantly between populations. The Okaloosa population had the highest mean stem density (1050 ± 188 stems/ha), while the Geneva population had the second highest (460 ± 60 stems/ha). The Baldwin population had the lowest mean stem density (275 ± 67 stems/ha). Further, The Okaloosa population had the highest mean basal area (2.3 ± 0.5 m^2/ha), while the Geneva population had the second highest (0.9 ± 0.1 m^2/ha). The Baldwin population had the lowest mean basal area (0.7 ± 0.2 m^2/ha). With respect to stems/ha and basal area within the midstory, the Baldwin population significantly differed from the Okaloosa population ($P = 0.001$ and $P = 0.001$, respectively). No other statistically significant differences were detected between populations.

Mean maximum canopy tree height across populations was 20.5 ± 0.6 m (*F* value = 1.171, $P = 0.341$). The mean canopy cover across all plots was 77.3 ± 3.1%. The Geneva population had the lowest average canopy cover (60.9 ± 0.7%), followed by the Okaloosa population (70.0 ± 3.9%) and the Baldwin population (85.1 ± 3.0%) (*F* value = 9.35, $P = 0.003$). The post hoc pair-wise comparison found the Baldwin County populations to have statistically significant different average canopy cover when compared to both the Geneva and Okaloosa populations ($P = 0.008$ and $P = 0.018$, respectively). No statistically significant relationships were found between the number of *F. milleri* ramets and the various microhabitat factors tested.

Soil Conditions

The average pH of all soil samples was acidic (4.860 ± 0.081; Table 3). The average pH of 0–10 cm samples was more acidic than the 10–30 cm samples (4.666 ± 0.101 and 5.054 ± 0.109, respectively). The Geneva population had the highest soil pH across both depths (5.454 ± 0.253). The Baldwin population had the second highest pH (4.834 ± 0.055). The Okaloosa population had the lowest soil pH across both depths (4.668 ± 0.184). The mean soil pH did differ across populations (*F* value = 7.409, $P = 0.007$). The Geneva population soil pH was significantly higher than the Baldwin and Okaloosa populations ($P = 0.006$ and $P = 0.017$, respectively). Further, the mean C:N ration varied between populations (*F* value = 5.234, $P = 0.022$). The Okaloosa population had the highest C:N ratio (35.3:1), which was significantly different from the Baldwin population ($P = 0.030$). No other significant differences were detected with respect to soil C:N ratio.

Soil textures associated with the sampled populations were determined to be sand, sandy loam, loamy sand, loam, and clay loam. The soil texture for all samples within the Geneva County population was sand. Similarly, most soil samples within the Okaloosa County population were also identified to be sand

Table 3.—Soil characteristics of the three sampled populations of *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae). Standard errors are presented parenthetically.

Population	Depth	Texture	pH	C:N ratio
All	All	Sand - Sandy Clay Loam	4.9 (0.1)	26.9 (1.8)
All	0–10	Sand - Sandy Clay Loam	4.7 (0.1)	27.8 (2.8)
All	10–30	Sand - Sandy Clay Loam	5.1 (0.1)	26.0 (2.4)
Geneva	All	Sand	5.5 (0.3)	21.3 (3.1)
Geneva	0–10	Sand	5.0 (0.2)	22.8 (3.5)
Geneva	10–30	Sand	5.9 (0.1)	19.8 (6.4)
Okaloosa	All	Sand - Sandy Loam	4.7 (0.2)	35.3 (4.6)
Okaloosa	0–10	Sand - Sandy Loam	4.3 (0.2)	37.6 (7.2)
Okaloosa	10–30	Sand - Sandy Loam	5.0 (0.2)	33.1 (6.3)
Baldwin	All	Sandy Loam - Loamy Sand - Sandy Clay Loam	4.8 (0.1)	23.5 (1.0)
Baldwin	0–10	Sandy Loam - Loamy Sand - Sandy Clay Loam	4.8 (0.1)	23.5 (1.6)
Baldwin	10–30	Sandy Loam - Loamy Sand - Sandy Clay Loam	4.9 (0.1)	23.4 (1.3)

(70% of samples), with the remaining samples considered sandy loam (20% of samples) and loam (10% of samples). The soil texture of the Baldwin population was identified as mostly a sandy loam (66% of samples), with the remaining characterized as loamy sand (22% of samples) and sandy clay loam (11% of samples).

Results from the Web Soil Survey were consistent with the results of the soil texture determined by feel (Thien 1979; Soil Survey Staff 2021). Soils were primarily classified as fine sandy loam or loamy fine sand that is well-drained to somewhat excessively well-drained. Soils were also classified as acidic by the web soil survey, consistent with the findings of the soil samples. Additionally, both the Baldwin and Okaloosa population had various muck soils that are poorly drained. All populations of *F. milleri* were not directly within a wetland according to the National Wetlands Inventory (U.S. Fish and Wildlife Service 2020). However, all populations were within approximately 200 m of a freshwater forested or shrub wetland (U.S. Fish and Wildlife Service 2020). No statistically significant relationships were found between the number of *F. milleri* ramets and the various soil microhabitat factors tested.

Habitat Suitability Model

The preliminary habitat suitability model had an average omission rate of 37.5% and an average area under the curve (AUC) of 0.6 (Figure 6). The area covered within the top bin (0.9–1) of habitat suitability accounted for only 0.5% of the total study area (625 km^2). The coastal regions of Alabama and Florida showed higher habitat suitability than inland regions. The mean temperature of the warmest quarter (bio10) contributed the most to the overall model (30.8%). Percent sand within the soil and precipitation in the warmest quarter (bio18) contributed the second (27.5%) and third most (20.8%) to the model, respectively.

DISCUSSION

Environmental stochasticity is the leading cause of extinction for plant species with small, fragmented populations (Matthies et al. 2004). Through personal communication with the local species expert, Dr. Ron Miller, it was determined that the three sampled populations were the three largest populations. Through our counts, 3060 ramets were found across all three populations in approximately 8.3 total ha. Of the 3060 ramets, 45% (1367 ramets) were found in a single subpopulation less than 0.5 ha in area within the Baldwin County site. As such, one stochastic event at this particular subpopulation could reduce the total population of *F. milleri* by 45%. Further, the Baldwin population alone accounts for 79% of the total number of ramets found in the three largest populations, which are located in only 4.5 ha of area. This concentrated distribution of *F. milleri* ramets in a small area makes the species particularly vulnerable to stochastic events. The relatively low number of ramets (3060) found across the three populations, and the small area in which they occupy raises concerns for the perpetuation of the species on the landscape.

Knapp et al. (2021) found 64% of extinct plants in the continental United States and Canada were single-site endemics, defined as having an area of occupancy ≤600 ha. While *F. milleri* would not currently be considered a single-site endemic according to their criteria, since it has more than one documented population, it could become a single-site endemic soon if active conservation and proper management are not prioritized. If *F. milleri*, or any rare and imperiled plant species, is to perpetuate on the landscape, simply preventing extinction cannot be the exclusive goal of conservation (Knapp et al. 2021). Instead, multiple, self-sustaining populations are needed. The number of genetically different genets is likely to be much lower than the number of ramets counted due to the rhizomal growth form of the species. Low genetic diversity could hinder the conservation of the species by making the populations more vulnerable to genetic drift, genetic bottlenecks, and inbreeding depression (Spielman et al. 2004). An understanding of the genetic diversity among these 3060 ramets is needed to better inform future conservation actions.

Fothergilla milleri produce seed capsules dispersed abiotically by gravity with no known animal or insect vectors for seed dispersal. Abiotic distribution via gravity may limit the ability of the species to spread and not allow the species to form new populations. Moreover, seed capsules found throughout the survey period appeared to be infected by an aphid (Figure 3b). The aphid is likely *Hamamelistes blackmani*, although no aphids were directly identified by the authors. No healthy, uninfected seed capsules were found in any of the sampled populations.

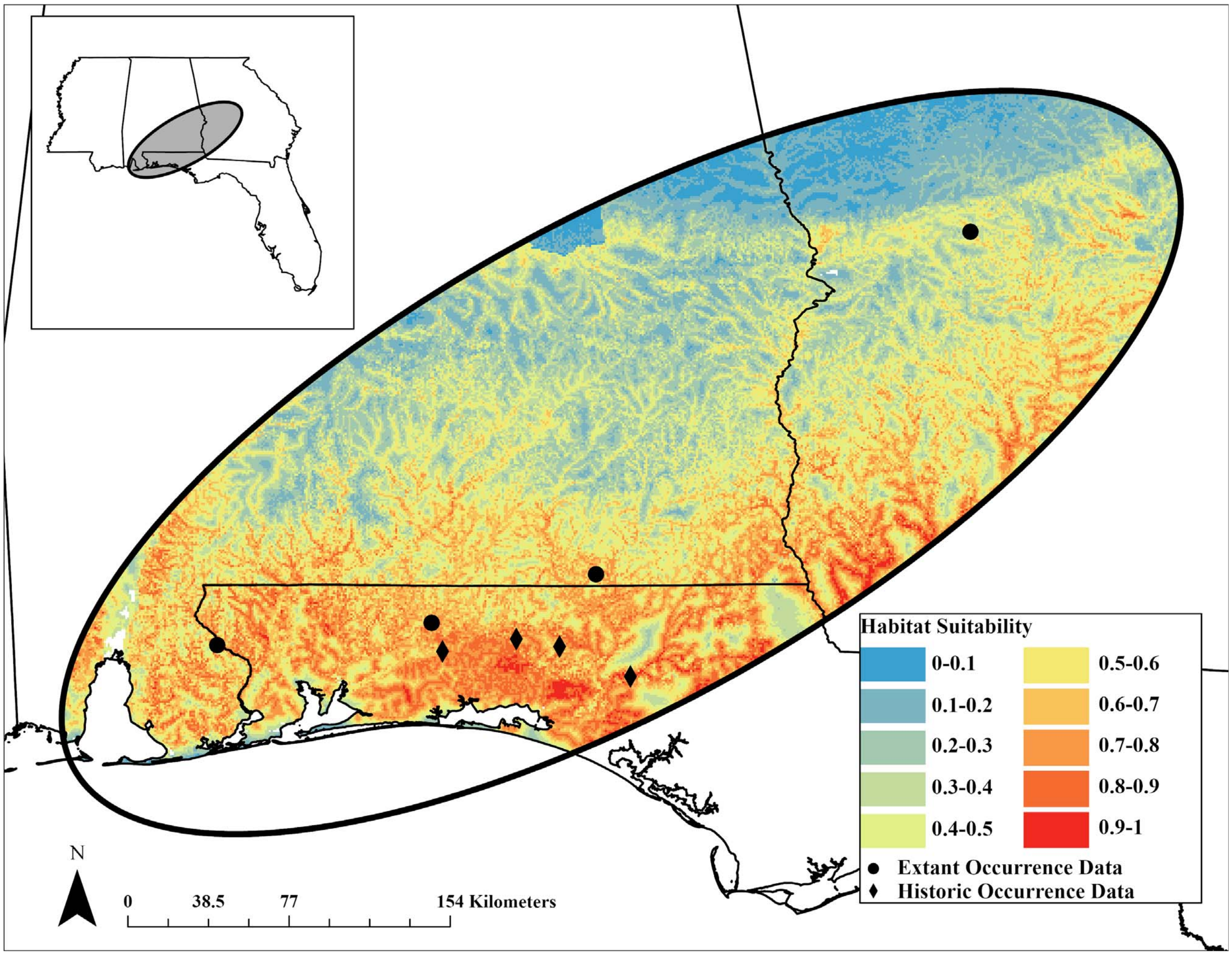

Figure 6.—The habitat suitability model developed within Maxent for *Fothergilla milleri* (W.D. Phillips & J.E. Haynes; Hamamelidaceae) from historical and extant occurrence points ($n = 8$) and 20 environmental variables. The study area is indicated by the gray shading. The model had an overall average omission rate of 37.5% and an AUC of 0.6.

This species of aphid has only recently been identified and appears to require *Fothergilla* spp. to complete its lifecycle. A post made in 2012 on the online forum BugGuide.net reports a morphologically similar gall on a *F. gardenii* in Okaloosa County, Florida (BugGuide 2021). This individual would likely now be considered *F. milleri* as opposed to *F. gardenii*. Based on the morphological similarity and species association, this is likely the same species of aphid found in the ramet count surveys. Seeds of American witchhazel (*Hamamelis virginiana* L.), which is also a member of the Hamamelidaceae family, have been infected with the aphid *Pseudanthonomus hamamelidis* (Dietz). In some cases, 76% of seed crops were infected (Steven 1981). While *F. milleri* can reproduce vegetatively, a lack of sexual reproduction could severely hamper regeneration and conservation efforts for the species. Identifying potential avenues for protecting *F. milleri* from the parasitism will need to be explored.

The results of this study support the habitat description Haynes et al. (2020) provided when first describing the species. However, this study provides additional valuable information about habitat that supports *F. milleri*. Haynes et al. (2020) describe the habitat of *F. milleri* as "sandy peat shrub bogs, seepages, dry longleaf pine woodlands, and the edge of *Cyrilla racemiflora* or *Taxodium ascendens* swamp forest." Although no *T. ascendens* was found within our study plots, all other habitat descriptions align with the results of this study. Additionally, Barger et al. (2013) described the habitat of *F. gardenii* within Baldwin County, Alabama, as "wet savannas, flatwoods, pocosins, and along the edges of pitcherplant bogs, baygalls, and shrub swamps," which is likely the same Baldwin County population sampled for this study and would likely now be considered *F. milleri*. Importantly, all studies have identified *F. milleri* habitat at the edge or transitional habitat between the flatwoods and bogs.

Fothergilla milleri and *F. gardenii* seem to share similar habitat requirements. The habitat of *F. gardenii* is described to be pine savannas and evergreen bogs, like that of *F. milleri* (Godfrey and Wooten 1981). Further, *F. gardenii* is a noted species associate of Atlantic white-cedar (Sheridan and Patrick 2003), which was also the third most abundant overstory species and fourth most abundant midstory species within the *F. milleri* vegetation plots.

The habitat suitability model presented in this study further supports the conclusion that *F. milleri* fills a unique niche in coastal forests. Only 625 km^2, or 0.5% of the total study area, was found to be in the highest bin of habitat suitability. The findings of this preliminary habitat suitability model aligned with the results from the soil sampling within populations of *F. milleri*. Percent sand in the soil contributed 27.5% to the overall model and was the second most important environmental variable. These results show soil type, particularly the sand component, is consistent across populations and potentially important for *F. milleri* establishment and perpetuation.

The area used in the habitat suitability model was intentionally minimized to avoid extrapolation beyond the bounds of the model. With the limited number of occurrence points available for use in the habitat suitably model, there was concern that straying too far from documented occurrences could result in inappropriate conclusions. Small numbers of occurrence records can be problematic when developing such models. However, species with few occurrence records are often the species most in need of habitat suitability modeling to inform accelerated conservation action before more occurrences can be found (Gaubert et al. 2006). Due to its more recent discovery, there are no reliable records of *F. milleri* in herbariums or within citizen science databases. Future habitat suitability models may benefit in time as more *F. milleri* records are established in both formal herbariums and citizen science databases.

The default parameters setting within Maxent have been shown to overfit models and in some situations, such as regularization multiplier and feature class, do not produce the best possible models (Phillips et al. 2006; Anderson and Gonzalez 2011; Radosavljevis and Anderson 2014). A systematic review of the models utilizing Maxent found 3.7% of studies evaluated both the regularization multiplier and the feature class as this study did (Morales et al. 2017). This habitat suitability model represents the first attempt at directing conservation efforts for *F. milleri,* including possible searches for new populations. Further, this model could inform conservation action for *F. milleri* by prioritizing areas of high habitat suitability for introduction or reintroduction.

Fothergilla milleri seems to grow in transitional zones between upland conifer forest dominated by loblolly pine and longleaf pine and wetland forests containing Atlantic white-cedar, water oak (*Quercus nigra* L.), and bald-cypress (*Taxodium distichum* (L.) Rich.). An analysis of the National Wetlands Inventory delineations further supports this conclusion. All subpopulations of *F. milleri* were within 200 m of a designated wetland, and many were close to or on the delineation line (U.S. Fish and Wildlife Service 2020). However, none were within the wetlands themselves. These unique transitional habitats could face a combination of disturbance threats from both uplands and wetlands. Many of the upland conifer stands adjacent to *F. milleri* subpopulations are managed pine plantations. Intensive forest management, such as nonselective midstory and ground cover herbicide application and harvesting operations, could negatively impact these *F. milleri* populations.

Many subpopulations of *F. milleri* are under a thick midstory of large gallberry and buckwheat trees. While the shade tolerance of *F. milleri* has not been quantified, anecdotal evidence from land managers suggests *F. milleri* may have a low tolerance of shade. If active management is not carried out, *F. milleri* populations may become heavily shaded and may eventually be outcompeted for both light and other resources. Haynes et al. (2020) discussed the need for regular fire to constrain competing vegetation in *F. gardenii* populations. Additionally, fire suppression has been cited as one of the major factors leading to habitat degradation in *F. gardenii* populations, some of which may now be considered *F. milleri* (Barger et al. 2013). Fire is likely needed to impede buckwheat tree and large gallberry within *F. milleri* populations to prevent the populations from becoming shaded out. Further research is needed into the role fire may potentially play in *F. milleri* regeneration to better inform conservation land management for the species.

The evidence suggests *F. milleri* is facing several threats including environmental stochasticity, possible limitations on sexual reproduction, and competition for light resources. Due to the small total population size and increasing threat, *F. milleri* may be a candidate for listing through the Endangered Species Act (§§17.61–17.63). Further evaluation is needed to determine *F. milleri*'s eligibility to be federally listed due to its small total population size, small number of populations, and possible limits on sexual reproduction. Nevertheless, research into both the role fire plays in the regeneration of the species, the species' ability to sexually reproduce, and genetic diversity and gene flow are all needed to fully understand the current conservation status of *F. milleri*. Concurrently, direct action to protect *F. milleri* is needed. Possible conservation measures include ex situ conservation in botanic gardens, cultivating the species to supplement current populations, establishing seed banks, growing in plant nurseries, and further protection of wild populations. Lastly, within wild populations, land management such as midstory or overstory reduction cuts as well as prescribed fire may be needed to prevent populations from becoming outcompeted for limited resources such as light and space.

CONCLUSION

Fothergilla milleri occupies a unique habitat in the transition between upland conifer forest and wetlands. Further, *F. milleri* likely requires specific soils that are acidic and have high sand content. *Fothergilla milleri* is facing multiple threats to its perpetuation. The most pressing being environmental stochasticity. One such event could eliminate nearly 79% of the ramets within the three largest populations. Further, it appears sexual reproduction is not currently taking place in the sampled populations of *F. milleri* due to the seed capsules infected by an aphid, likely *Hamamelistes blackmani*. Also, due to the small population size and disjunct nature of those populations, a lack of genetic diversity is a concern that needs further research. Lastly, many subpopulations of *F. milleri* are under thick midstories. Fire may be needed to open the overstory and midstory so *F. milleri* is not shaded out in these subpopulations. A lack of suitable habitat may further hinder conservation efforts. Based on the identified threats and very specific habitat of *F. milleri*, it is likely active and intentional conservation efforts are needed for *F. milleri* to remain on the landscape in perpetuity.

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Clayton W. Hale was a graduate research assistant in the Department of Forestry at Mississippi State University when this work took place. He holds a B.S. in Forestry from the University of Tennessee, Knoxville, and a M.S. in Forestry from Mississippi State University. His research interests include forest ecology, habitat suitability models, plant community assemblages, plant invasion, and the conservation of rare and imperiled plant species.

Joshua J. Granger is an Assistant Professor in the Department of Forestry at Mississippi State University. His research interests focus on forest ecology and quantitative silviculture, with emphases on forest regeneration and conservation of native plant communities and natural resources in the eastern United States. His primary interests are to combine habitat suitability modeling and other quantitative techniques with manipulative experiments to pinpoint optimum habitat conditions for economically important timber species, wildlife, and rare and imperiled species, in order to provide information that will aid landowners, managers, and government officials in sustaining representative forest ecosystems and the natural resources they provide for future generations.

Courtney Siegert is an Associate Professor in the Department of Forestry at Mississippi State University. Her research program examines how water and nutrient cycles are affected by natural and anthropogenic disturbances in forest ecosystems.

Sandra B. Correa is an Assistant Professor in the Department of Wildlife, Fisheries, and Aquaculture at Mississippi State University. Her research focuses on understanding the various ecological roles played by wetland forest ecosystems, including supporting biodiversity, aquatic food webs, and fisheries. Moreover, she seeks to investigate how climate change is altering these ecological roles and whether wetland forests can contribute to mitigating the detrimental effects of climate change at local and regional scales.

Janice L. DuBien is an Associate Professor of Statistics in the Department of Mathematics and Statistics at Mississippi State University. Her research focuses on applied statistics.

Caleb D. Goldsmith was a graduate research assistant in the Department of Forestry at Mississippi State University. His research interests focus on forest and fire ecology, invasive plant species, and the conservation of rare and imperiled plant species.

Will Kruckeberg was a graduate research assistant in the Forest Soils and Hydrology Lab at Mississippi State University. He received his B.S. in Forestry from Stephen F. Austin State University in Nacogdoches, Texas. His research interests include forest ecology, forest soils and hydrology, and fire ecology.

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