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Research Article

Evidence of Mesophication in the Georgia Piedmont

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ABSTRACT

Across the eastern United States several trends are altering the composition of forest. One important trend is that of oaks (*Quercus* spp.) being lost and oak-dominated forests gradually shifting to other species compositions. One leading hypothesis for the recent demise of oaks is the process of mesophication, by which, largely due to fire suppression, fire-adapted species and plant communities are being replaced by more mesophytic species/community types. Recent work has suggested the mesophication process is a feedback loop, and mesophytic species create microclimates and fuel beds that are less likely to burn, thereby further enhancing the effects of the mesophication process and allowing mesophytic species to further dominate. Most studies detailing mesophication have taken place in the Mid-Atlantic, Midwest, and Cumberland Plateau areas of the eastern United States, with very few providing evidence within the Southeastern Piedmont. Utilizing a newly established 12 ha forest dynamics plot in Athens, Georgia, USA, we provide evidence that the mesophication process is taking place in a mixed pine-hardwood Southeastern Piedmont Forest. Within the study site oaks represented 1% of saplings, while mesophytic species accounted for 96% of saplings. Conversely, oaks accounted for 47% of stems in the overstory, while mesophytic species represented 31% of stems in the overstory. The data suggest an “oak bottleneck,” a phenomenon closely associated with mesophication. This work informs long-term land management decision making regarding mixed pine-oak stands for both conservationists and the forest industry.

Index term: fire; mesophytic; oak; pine; pyrophytic

INTRODUCTION

Oaks (*Quercus*) have long been considered a foundational genus within the forests of eastern North America (Hanberry and Nowacki 2016). Once dominating many of those forests, many ecologically and economically important oak species are currently in a period of decline in terms of both density and importance value (Fei et al. 2011), resulting in shifts in canopy composition across a broad range of forest types. Parallel trends have been observed in the regeneration of many forests, with some studies reporting even lower proportions of oaks in the sapling and midstory stages of development (Fei et. 2011; Dyer and Hutchinson 2019). Of concern to foresters and conservationists alike, scarcity of oaks in the sapling and midstory suggest a lack of regeneration potential to replace aging overstory individuals. Further, the loss of oak species in the eastern United States could have dire consequences for wildlife populations due to the loss of hard mast production (McShea et al. 2007). This phenomenon currently playing out at sites across the eastern United States is known as the “oak bottleneck” (Nowacki and Abrams 1992). The leading hypothesis to explain this decline in oaks is the process of mesophication (Alexander et al. 2021).

Mesophication is the process by which pyrophytic species, such as oaks and pines (*Pinus*), are replaced by mesophytic species, such as elm (*Ulmus*) and maples (*Acer*). Pyrophytic species are defined as those species that have life histories closely associated with fire, whereas mesophytic species have difficulties surviving in fire-prone habitats. The process and implications of mesophication in the forests of the eastern United States has been an active area of research in recent years (Nowacki and Abrams 2008; Alexander et al. 2021).

While fire suppression policies are likely the cause of initiating the mesophication process, once mesophication begins, a self-perpetuating feedback loop is established, making it ever more difficult for stands to maintain oaks and other pyrophytic species. Alexander et al. (2021) describes the positive feedback process in which, as mesophytic species become established, they create more favorable microclimates for more mesophytic individuals to become established. Through altering the microclimates, mesophytic species create conditions that suppress fires. Conversely, pyrophytic species promote fire in their surrounding microclimates (Alexander et al. 2021).

Most studies describing mesophication have occurred in the Central Hardwood Region of the eastern United States, with a minority describing mesophication in the eastern Piedmont. Further, no study known to the authors has described mesophication in the Georgia Piedmont. The objective of this study is to quantify the regeneration component of the woody plant community in a mature secondary pine-hardwood forest on the Georgia Piedmont to assess if the site is in the process of mesophication. Understanding the similarities and differences of the mesophication process across ecological systems will prove critical to developing system-specific best management practices to prevent and reverse landscape level losses of pyrophytic species, including economically and ecologically valuable oak species.

METHODS

Study Site

In 2015, a 12 ha permanent plot, known as The University of Georgia Forest Dynamics Plot (UGA FDP), was established at the State Botanical Garden of Georgia south of Athens, Georgia, USA (33.9015N, 83.3789W). The land was purchased by the University of Georgia in 1936; however, little is known about the site pre-1968 (Zenoble 2021). Aerial photography from 1938 suggests that roughly half the site was used for agriculture and the other half was forested. However, by 1951 the site was a closed canopy forest suggesting the successional age of the study site is currently at least 70 y, with some areas over 80 y old (Zenoble 2021). Additionally, there have been no known prescribed burns or wildfires within the site (Zenoble 2021). The study site is within the Southern Outer Piedmont level IV ecoregion (Griffith et al. 2001). The Piedmont is described as the transitional zone between the Appalachian Mountains and the Coastal Plain (Griffith et al. 2001). Soils within the site are mostly Madison sandy loam (53.8%) and Louisburg loamy sand (22.2%) with minor components of Pacolet sandy clay loam (15.1%) and Pacolet sandy loam (7.9%) (Soil Survey Staff 2020; Zenoble 2021). Although not quantified in this study, deer browsing is prevalent within the study site, which could contribute to forest regeneration dynamics.

Woody Vegetation Sampling

In 2018 and 2019, a 100% inventory of all woody stems >5 cm at breast height (1.37 m) within the study site was conducted. All stems >5 cm at breast height were tagged, identified to the species level (or genus level if species identification was not possible), and the diameter at breast height was recorded (Zenoble 2021). Additionally, in the fall of 2021 a survey of woody stems 1–4.9 cm at breast height was conducted. For the survey, 30 plots were randomly placed throughout the study site. Each plot was 0.05 ha in size. Within each plot, all stems 1–4.9 cm at breast height were identified to the species level (or genus level if species identification was not possible) and the diameter at breast height was recorded.

Data Analysis

To determine if mesophication is occurring within the study site all species were grouped either as mesophytic, xerophytic (similar to pyrophytic species), or other. A species was defined as mesophytic if a source in the primary literature could be found defining it as such (Table 1). To further support the assertion of a species being mesophytic, a column is provided of citations that categorize the species as a pyrophobe. Pyrophobic species often share similar tendencies as mesophytic species. It should be noted, *Sassafras albidum* ((Nutt.) Nees) is categorized as a mesophytic species for this study, which contradicts the pyrophilic designation provided by Thomas-Van Gundy and Nowacki (2013) and Nowacki and Abrams (2015). This is because Alexander et al. (2021) cites *Sassafras albidum* as an indictor species of the mesophication process. Similarly, *Crataegus* and *Oxydendrum arboretum* ((L.) D.C.) are considered pyrophilic by Thomas-Van Gundy and Nowacki (2013) but categorized as other for the purposes of this analysis. Oaks, pines, and hickories (*Carya*) were considered xerophytic. Lastly, species were grouped as "other" if a primary source could not be found describing it as mesophytic or xerophytic. The stems were additionally broken into three size classes based on their diameter at breast height—saplings (1–4.9 cm), midstory (5–20 cm), and overstory (>20 cm)—to assess differences in species, or designated group, composition between the different size classes. Due to the difference in methodology between the 100% inventory and sample plots, all stem counts are reported on a stems/ha basis. Standard errors are also presented parenthetically where appropriate for all average stems/ha results. A one-way analysis of variance (ANOVA) was used to test for differences in mean stem density between size classes and mean basal area between size classes. Additionally, an ANOVA was used to test for mean differences between species densities and basal area within the three size classes. An alpha level of 0.05 was used to determine statistical significance (online Supplement).

RESULTS

In total, across all size classes, 1135 (±291) stems/ha were found within the study site. The midstory size class had the highest density of stems (546 ± 115 stems/ha). The sapling size class had the second highest density of stems (344 ± 124 stems/ha), while the overstory had the lowest density (245 ± 52 stems/ha). The midstory density was significantly different than both the overstory ($P < 0.001$) and sapling ($P < 0.001$) classes. However, the sapling and overstory classes did not vary significantly ($P = 0.293$). The species with the highest density in the sapling size class was winged elm (106 ± 34 stems/ha; *Ulmus alata* Michx.), followed by eastern hophornbeam (67 ± 23; *Ostrya virginiana* (Mill.) K. Koch) and Florida maple (48 ± 16; *Acer floridanum* (Chapm.) Pax), respectively (Figure 1c). The midstory size class followed a similar trend with winged elm (81 ± 22 stems/ha), red maple (79 ± 10 stems/ha; *Acer rubrum* (L)), and eastern hophornbeam (70 ± 13 stems/ha) having the three highest stem densities (Figure 1b). Within the overstory size class, white oak (*Quercus alba* L.) was most abundant in terms of number of stems (53 ± 6 stems/ha), while southern red oak (33 ± 10 stems/ha; *Quercus falcata* Michx.) and loblolly pine (25 ± 7 stems/ha; *Pinus taeda* L.) had the second and third highest densities, respectively (Figure 1a).

Basal area followed a similar trend to stem density with the midstory representing a total basal area of 4.58 ± 0.84 m^2/ha, while the overstory represents a total basal area of 28.88 ± 6.96 m^2/ha. Red maple had the highest basal area (0.67 ± 0.08 m^2/ha), while sweetgum (0.56 ± 0.12 m^2/ha; *Liquidambar styraciflua* L.) and winged elm (0.50 ± 0.12 m^2/ha) accounted for the second and third highest basal area within the midstory, respectively. The overstory species with the highest basal area was white oak (6.61 ± 0.82 m^2/ha) while southern red oak (3.90 ± 1.12 m^2/ha) and tulip-popular (3.61 ± 0.81 m^2/ha; *Liriodendron tulipifera* L.) had the second and third highest basal area in the overstory. Lastly, the sapling class had the least basal area with 0.29 ± 0.10 m^2/ha. Winged elm had the highest basal area in the sapling class (0.10 ± 0.03 m^2/ha) while eastern hophornbeam (0.05 ± 0.02 m^2/ha) and Florida maple (0.03 ± 0.01 m^2/ha) had the second and third highest

Table 1.—Species classified as mesophytes or other to analyze if mesophication is occurring within the University of Georgia Forest Dynamics Plot (UGA FDP). If a source in the primary literature could be found identifying a species as a mesophyte it was considered as such; those sources are listed. Species found within the UGA FDP that were not in the *Quercus*, *Pinus*, or *Carya* genera and a source could not be found identifying them as a mesophyte were listed as other.

Species	Mesophytes	Pyrophobes
Acer floridanum	Alexander et al. (2021)	Nowacki and Abrams (2015)
Acer leucoderme	Alexander et al. (2021)	Nowacki and Abrams (2015)
Acer negundo	Alexander et al. (2021)	Nowacki and Abrams (2015)
Acer rubrum	Alexander et al. (2021)	Nowacki and Abrams (2015)
Acer saccharinum	Alexander et al. (2021)	Nowacki and Abrams (2015)
Amelanchier arborea	Thomas-Van Gundy et al. (2018)	Thomas-Van Gundy and Nowacki (2013)
Carpinus caroliniana	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Cercis canadensis	Galgamuwa et al. (2019)	Nowacki and Abrams (2015)
Cornus florida	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Fagus grandifolia	Alexander et al. (2021)	Nowacki and Abrams (2015)
Fraxinus americana	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Fraxinus pennsylvanica	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Ilex opaca	Kreye et al. (2013)	Thomas-Van Gundy and Nowacki (2013)
Juniperus virginiana	Hoff et al. (2018)	Nowacki and Abrams (2015)
Liquidambar styraciflua	Alexander et al. (2021)	Nowacki and Abrams (2015)
Liriodendron tulipifera	Alexander et al. (2021)	Nowacki and Abrams (2015)
Magnolia acuminata	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Morus rubra	Hart and Kupfer (2011)	Nowacki and Abrams (2015)
Nyssa sylvatica	Nowacki and Abrams (2008)	Nowacki and Abrams (2015)
Ostrya virginiana	Thomas-Van Gundy et al. (2018)	Nowacki and Abrams (2015)
Prunus serotina	Alexander et al. (2021)	Nowacki and Abrams (2015)
Sassafras albidum	Alexander et al. (2021)	
Tilia americana	Palus et al. (2018)	Nowacki and Abrams (2015)
Ulmus alata	Alexander et al. (2021)	Nowacki and Abrams (2015)
	Other	
Catalpa bignonioides		
Crataegus spp.		
Diospyros virginiana		Nowacki and Abrams (2015)
Elaeagnus umbellata		
Gymnocladus dioicus		
Ligustrum sinense		
Oxydendrum arboreum		
Platanus occidentalis		Nowacki and Abrams (2015)
Vaccinium arboreum		
Vaccinium elliottii		
Viburnum rufidulum		

basal area within the sapling class, respectively. All three size classes varied significantly from one another with respect to mean basal area ($P < 0.001$ for all comparisons).

Mesophytic species (e.g., winged elm, sweetgum, red maple, and Florida maple) dominated both the sapling and midstory size classes, while pyrophytic oaks had the highest proportion of stems/ha in the overstory (Figure 2). In the sapling size class, mesophytic species were the largest group (96%), while hickories (2%), oaks (1%), and pines (0%) made up very little of the sapling size class. Within the midstory size class mesophytic species made up a smaller percentage of the overall stems (85%) than in the sapling size class, but still had the highest stem density of any of the groups. Oaks (7%) have a slightly greater representation in the midstory size class than in the sapling size class; however, the percentage of hickories did not change from the sapling size class to the midstory (2%). Additionally, pines were sparse within the midstory size class (2%). Lastly, oaks had the highest density in the overstory size class (47%), while mesophytic species had the second highest (31%). Pines (11%) and hickories (7%) both made up a somewhat greater proportion of the overstory compared to the sapling and midstory size classes.

DISCUSSION

The leading hypothesis to explain the shift in plant communities away from oak dominated forest and toward a mesophytic community is a lack of fire on the landscape (Nowacki and Abrams 2008). Unfortunately, we do not know the fire regime of this study site pre-1936; however, based on landscape level generalizations, this region historically would have seen frequent, low-to-mid severity fires (Nowacki and Abrams 2008). We do know that this site has not burned since 1968 and examination of periodic aerial photos between 1936 and 1968 show no indication of substantial fire (Zenoble 2021). Due to the likely agricultural land use pre-1936, fires could have

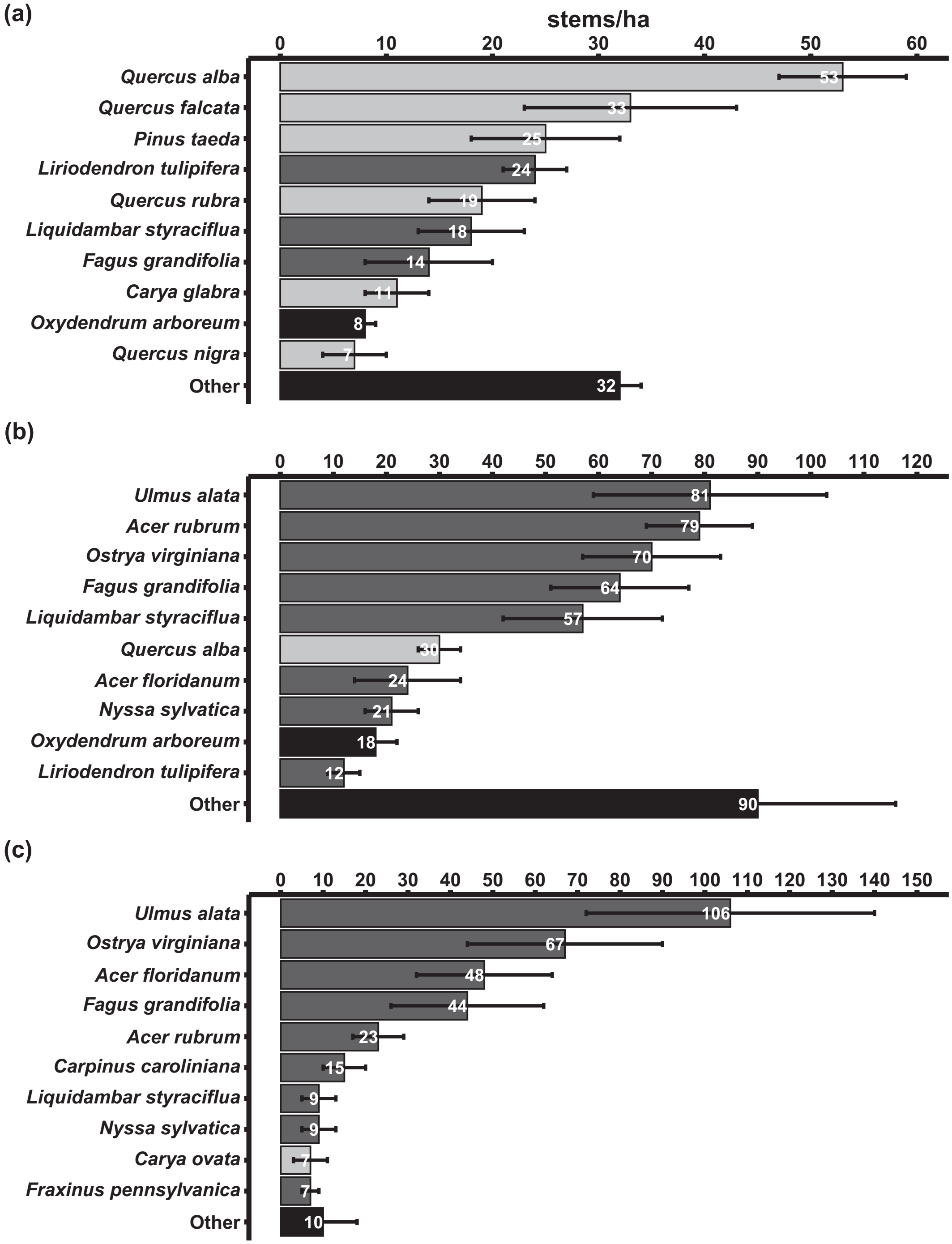

Figure 1.—(a) Stems/ha of overstory tree species (≥20 cm at dbh) within the 12 ha permanent plot, known as The University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Garden of Georgia south of Athens, Georgia, USA (33.9015N, 83.3789W). (b) Stems/ha of midstory species (5–20 cm dbh) within the UGA FDP. (c) Average stems/ha of sapling species (1–4.9 cm dbh) within the UGA FDP. Light gray shading indicates the species is pyrophytic, dark gray indicates the species is mesophytic, and black indicates the species was categorized as other.

been used to clear the sections of the study site that were used for agriculture, which could have burned into the portions of the study site that were forested. Agricultural burns were commonplace in the southeastern United States until the federal government adopted a policy of fire suppression in the 1920s (Fowler and Konopik 2007). These agricultural burns would have been similar to the frequent, low- to mid-severity fires of the historical fire regime (Nowacki and Abrams 2008). These fires would therefore be advantageous for both oak and pine development into the overstory, while reducing survival of the mesophytic species. Once the study site was bought by the University of Georgia, these types of fires have apparently no longer taken place, explaining older established oaks and pines in the overstory and so few in the sapling and midstory size

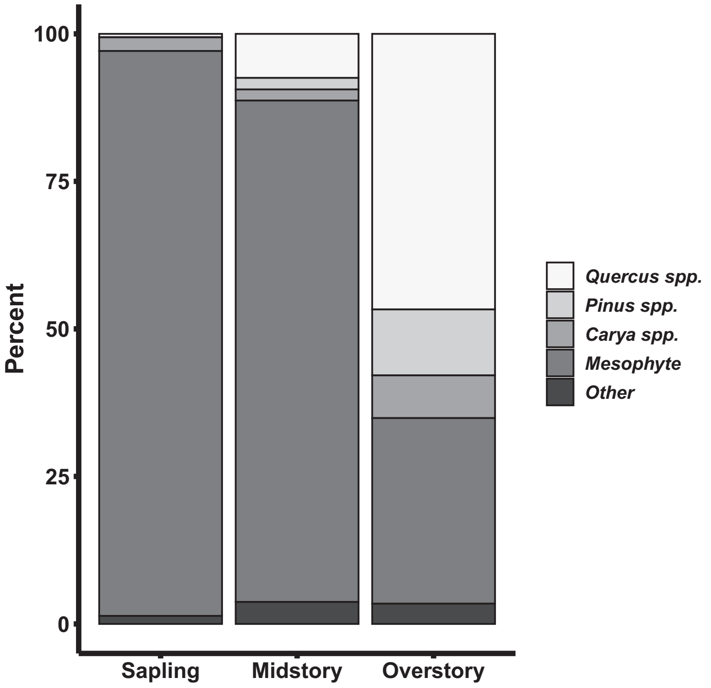

Figure 2.—Proportion of stems categorized as the appropriate genus (*Quercus*, *Pinus*, or *Carya*), a mesophyte, or other for three size classes, overstory (>20 cm dbh), midstory (5–20 cm dbh), and sapling (1–4.9 cm dbh) within the University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Garden of Georgia south of Athens, Georgia, USA (33.9015N, 83.3789W).

classes. However, without knowing precisely the past fire regime other possible explanations for the current composition of the overstory cannot be dismissed. Although fire suppression is a likely component, age-specific growth and mortality rates between the pyrophytic and mesophytic species within the developing stand could account for the current composition.

Alexander et al. (2021) describes three case studies of apparent mesophication. The first is in the Indiana Dunes National Park, Indiana (see also Sanders and Grochowski 2013), second within Bernheim Arboretum and Research Forest, Kentucky, and third at Spirit Hill Farm, Mississippi, USA. The size classes used by Alexander et al. (2021) are slightly different than those used for this study, specifically the midstory is considered to be 10–20 cm whereas ours is 5–10 cm. Through broad comparison, a similar trend can be clearly seen between this study and the three presented in Alexander et al. (2021). The sapling and midstory size classes have a relatively high percentage of mesophytic stems and a low percentage of oaks. The main difference between the three studies presented in Alexander et al. (2021) and this study is the percentage of oaks in the overstory. The range for the percentage of oaks in the overstory presented in Alexander et al. (2021) is ~60% to well over 75%, while the percent of oaks in overstory of this study is 47%, albeit oaks still had the highest representation. This difference could be explained by the number of pines in the overstory of this study (11%). Pines were not reported in the Alexander et al. (2021) case studies; however, pines are known to be a fundamental component of Southern Outer Piedmont Forest (Griffith et al. 2001). The addition of a pine component in the overstory could partially explain this difference. Surrette et al. (2008) found periodic low-intensity fires likely act as a filter to suppress mesophytic species establishment and maintain forest composition in the mixed oak-pine upland coastal plain of northern Mississippi. A similar scenario is possible in the mixed oak-pine uplands of the Georgia Piedmont, where this study took place and could account for the current lack of pines and oaks in the midstory and sapling classes. Another possible explanation of this difference is the mesophication process itself. The study site could be going through later stages of the mesophication process. The overstory oaks and pines could be dying out of the overstory, and because of a lack of oaks and pines in the midstory, are being replaced by more mesophytic species. This phenomenon is known an "oak bottleneck," which is when there is insufficient oak regeneration in the sapling and midstory classes to replace those that die in the overstory (Nowacki and Abrams 1992; Alexander et al. 2021)

Although not quantitively measured, Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus.) was prevalent throughout much of the study site (Figure 3). Japanese stilt grass is an annual, shade tolerant grass native to parts of Asia, and well-known invader of southeastern forest (Barden 1987). Japanese stilt grass has been shown to lower plant diversity within invaded sites (Flory et al. 2007; Adams and Engelhardt 2009). The shade tolerant nature of Japanese stilt grass could allow for its expansion as the site continues the mesophication process, further limiting the plant diversity within the site. Additionally, the presence of Japanese stilt grass on the site could limit potential management options due to its ability to proliferate in disturbed habitats (Brewer et al. 2015). For example, Brewer et al. (2015) found Japanese stilt grass proliferated post-fire treatment. Lastly, recent research has indicated Japanese stilt grass could impact the growth and biomass accumulation of certain hardwood species during development (Goldsmith et al. 2023).

The implications of mesophication are not entirely understood and are in need of further research. An obvious possible implication is the loss of hard mast as a food source for wildlife species. It is currently unclear if mesophytic species will be able to support wildlife populations to the same extent as pyrophytic, hard mast–producing species. Further, little is known of the implications of carbon sequestration with respect to mesophication. In light of a changing climate, such implications within eastern oak forests are critical to understand (Iverson et al. 2019).

Along with Zenoble (2021), this is the first evidence known to the authors that documents mesophication in the Georgia Piedmont. Most studies have shown mesophication in more hardwood dominated systems, rather than the mixed pine and hardwood forest of the Georgia Piedmont. The work indicates land managers and conservationists may need to account for mesophication in a wider range of the eastern United States than previously thought. Further, this study tests one

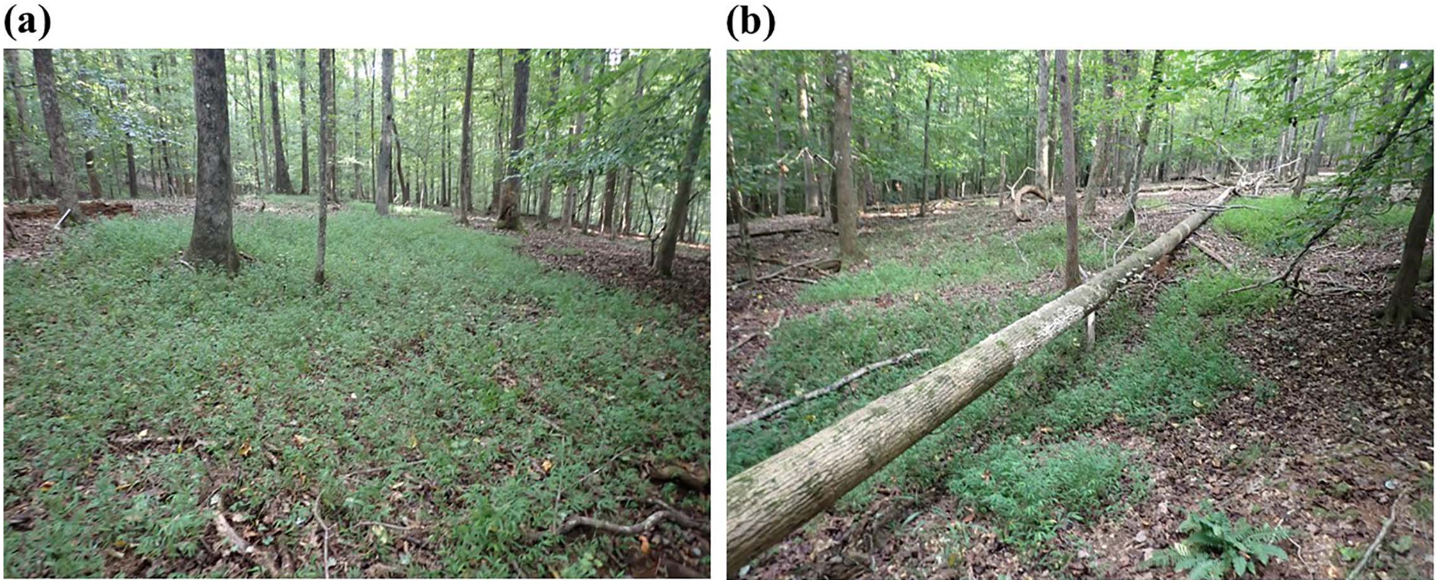

Figure 3.—Japanese stilt grass (*Microstegium vimineum* (Trin.) A. Camus.) invasion within the University of Georgia Forest Dynamics Plot (UGA FDP) at the State Botanical Garden of Georgia south of Athens, Georgia, USA (33.9015N, 83.3789W).

prediction of the mesophication hypothesis, that pyrophytic overstory species are being replaced by midstory mesophytic species due to fire suppression. Further research is needed to quantify the abiotic changes associated with mesophication, such as increased soil moisture, decreased temperature, and decreased flammability, to test other predictions of the mesophication hypothesis. Lastly, this research relies heavily on the assumption that stems in smaller size classes are representative of the future overstory, which is commonplace in forestry thinking. Although we believe this is a reasonable assumption, long-term forest dynamics studies are needed to confirm this assumption.

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Chris J. Peterson is a plant ecologist and professor in the Department of Plant Biology at the University of Georgia. His research focuses on a variety of topics related to forest wind disturbance and long-term carbon dynamics of eastern U.S. forests. He initiated and maintains the UGA FDP.

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