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Fire intolerance of invasive woody plants evidenced by bark thickness: implications for invasion in fire-suppressed forests

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Abstract

Background Frequent low-intensity fires historically shaped forest composition and structure in the southeastern United States of America (USA). However, in modern times, fire suppression has inadvertently facilitated the recruitment of mesophytic trees and potentially the invasion of non-native woody plants. In this study, we selected twelve woody broadleaved plants from forested areas of South Carolina and categorized them into three groups: (1) non-native invasive species, (2) native pyrophytic species, and (3) native mesophytic species. We used these categories to examine bark thickness—one critical determinant of fire tolerance—across a spectrum of stem sizes (16.3 mm < DBH < 69.4 mm).

Results Across all species, pyrophytic species consistently exhibited the thickest bark at all measurement heights, followed by invasive species, while mesophytic species had the thinnest bark. Invasive and mesophytic species displayed similar absolute and relative bark thickness values and demonstrated comparable trends in bark thickness variation with increasing stem size. Absolute bark thickness decreased with increasing height along the stem in all groups; however, pyrophytic species exhibited a more pronounced decline in bark thickness from the ground line to breast height compared to mesophytic and invasive species. For pyrophytic species, relative bark thickness at the ground line decreased sharply with increasing stem diameter, indicating a significant early-life investment in bark development.

Conclusions The congruence in absolute and relative bark thickness patterns between mesophytic and woody invasive plants along both horizontal (DBH) and vertical (height) gradients indicates that fire suppression may have helped to facilitate invasive species establishment and spread and that the restoration of historical fire regimes (e.g., repeated surface fire), suggested for reducing mesophytes, could aid in the management of woody invasive plants.

Keywords *Carya*, Fire suppression, Fire tolerance, Hickory, Oak, Prescribed fire, *Quercus*

Resumen

Antecedentes Incendios frecuentes de baja intensidad han modelado históricamente la estructura y composición de de los bosques en el sudeste de los Estados Unidos. Sin embargo en tiempos modernos, la supresión de los fuegos ha inadvertidamente facilitado el reclutamiento de árboles mesofíticos y potencialmente la invasión de plantas

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leñosas no nativas. En este estudio, seleccionamos doce especies arbóreas latifoliadas de áreas forestadas de Carolina del Sur y las categorizamos en tres grupos: (1) especies invasivas no nativas, (2) especies pirófilas nativas, y (3) especies nativas mesofíticas. Usamos esas categorías para examinar el ancho de la corteza -un determinante crítico de la tolerancia al fuego- a través de un espectro de tamaños de los tallos (16,3 mm DBH 69,4 mm).

Resultados Entre todas las especies analizadas, las pirofíticas exhibieron consistentemente la corteza más ancha en todas mediciones en altura, seguidas por las especies invasoras, mientras que las especies mesofíticas tuvieron la corteza más fina. Las especies mesofíticas y las invasoras mostraron similares valores de ancho tanto absolutos como relativos y demostraron tendencias comparables en la variación del ancho de la corteza al incrementarse el tamaño del tallo. El valor de ancho absoluto de la corteza decreció con el incremento de la altura en todos los grupos: por supuesto, las especies pirofíticas exhibieron una declinación más pronunciada en el ancho de la corteza desde la línea del suelo hasta la altura del pecho comparado con especies mesofíticas e invasoras. Para las especies pirofíticas, el ancho relativo de la corteza a nivel del suelo decreció rápidamente con el incremento del diámetro del tallo, indicando una inversión en el desarrollo de la corteza a edades tempranas.

Conclusiones La congruencia en los patrones absolutos y relativos del ancho de la corteza entre especies mesofíticas y plantas arbóreas invasoras, tanto en gradientes a nivel horizontal (DBH) como vertical (altura), indica que la supresión del fuego puede haber ayudado a facilitar el establecimiento y la propagación de especies invasoras, y que la restauración de los regímenes de fuego históricos (i. e. repetición de fuegos superficiales), sugeridos para reducir las mesófitas, pueden ayudar en el manejo de plantas leñosas invasoras.

Background

Fire plays a critical role in shaping natural communities by influencing the structure, composition, and dynamics of woody species (Chang et al. 2007; Keeley et al. 2008). Ecosystems that have evolved with fire are globally widespread and characterized by fire intervals shorter than the lifespan of dominant plants, necessitating adaptive traits for species persistence (Krawchuk et al. 2009; Pausas 2015). In the eastern United States of America (USA), both the burning practices of indigenous peoples and natural wildfires have played a role in preserving the distinctive open-canopy structure of open pine and oak woodlands and savannas (Baldwin et al. 2023). For example, fire helps pitch pine (*Pinus rigida* Mill.) by reducing shade-tolerant competitors, ensuring its seeds can sprout in sunlight and bare soil (Lee et al. 2019). Similarly, longleaf pine (*Pinus palustris* Mill.) demonstrates a remarkable capacity to withstand fire as a juvenile, an essential attribute for its continued prevalence in very frequently burned savannas (Wang and Wangen 2011; Pile et al. 2017a; Knapp et al. 2018). The dynamic relationship between fire, including frequency, severity, and seasonality, and the biotic community is critical not only to the survival and distribution of individual plant species but also to the overall structure and composition of the forest. Understanding this interaction is vital for the effective management and conservation of fire-dependent ecosystems (Christianson et al. 2022; Kiel et al. 2023; Singh et al. 2023).

Due to population growth and Changes associated with the land-use practices of European settlers, fire suppression became common and dramatically altered the landscape of many fire-maintained natural communities. The onset of industrial logging in the late nineteenth century, combined with active fire suppression policies since the early 1900s, has led to changes in the structure and composition of eastern forests in the USA, whereby fire-adapted and fire-tolerant species are being replaced by highly competitive and aggressive fire-intolerant trees and shrubs. Mesophication refers to the forest succession process whereby ecosystems derived from frequent fire transition to closed-canopy forests dominated by shade-tolerant species that are less receptive to burning (Fowler and Konopik 2007; Nowacki and Abrams 2008; Varner et al. 2021; Pile Knapp et al. 2024). The overriding fire regime influences the composition and structure of natural communities, and the suite of representative pyrophytic traits in an ecosystem is conferred by its overall effect (Varner et al. 2021). For example, in the absence of very frequent fire, species such as longleaf pine are replaced by less fire-tolerant oaks (*Quercus* spp.) and mesophytic red maple (*Acer rubrum* L.). When fire regimes are less frequent, oaks persist along with pine developing open, mixed pine-oak woodlands. Changes in species compositions alter the flammability of surface fuels, further reinforcing transitions in forest composition and structure (Jamison et al. 2023; Pile Knapp et al. 2024). The positive feedback loop created by fire suppression allows fewer fire-tolerant species to establish and recruit, reducing the likelihood of fire and perpetuating the cycle of mesophication (Nowacki and Abrams 2008; Shearman et al. 2018). For example, oak-dominated forests historically developed under a regime of intermediate and intermittent surface fire, maintaining their dominance over mesophytic species but allowing their recruitment across the landscape (Frost 1998; Knapp et al. 2022).

Although not well-studied, in the southeastern USA, alterations to historic frequent fire regimes were coincident with the introduction and spread of many non-native, invasive plants. Fire suppression may have inadvertently facilitated ecological conditions that benefited invasive woody plants, which often can outcompete native plants, significantly altering biodiversity and ecosystem function. Invasion by woody plants often results in dense monocultures, overshadowing and suppressing the growth of native understory flora and tree regeneration, leading to reduced plant diversity and abundance and failure to recruit adequate tree regeneration (Vickers et al. 2019; Turner et al. 2022; Vaughn et al. 2024). These woody invasive plants are often highly adaptable and can quickly colonize disturbed habitats, particularly in environments where the historical fire regime has been suppressed (Pile et al. 2019; Pile Knapp et al. 2023). Keeley et al. (2008) examined the impact of fire severity on invasive plants in shrublands of California and found that high-severity fires reduce the proportion of invasive plants, suggesting that strategic fire use may be an effective tool in managing invasive plant populations. However, they also noted that low-intensity fires might promote invasive spread, which is of particular concern for invasive grasses (Yager et al. 2010; Tomat-Kelly et al. 2021), underscoring the need for fire management that balances the control of invasive plants with the preservation of native ecosystems. For woody invasive plants, greater control of invasive populations may occur when growing-season burns result in physiological damage or when fire targets seedlings or saplings (Grace 1998; Richburg et al. 2004; Pile et al. 2017b; Rebbeck et al. 2019). Further, plant communities that have maintained their historic fire regime may have limited plant invasion due to repeated fire impeding invasive plant establishment or fire precluding invasive plant reproductive capacity (Simberloff 2001; Just et al. 2017; Pile Knapp et al. 2023). The complexity of fire's role in ecosystems highlights the importance of nuanced fire management policies that adapt to the specific conditions of each forest type and the challenges presented by invasive plants. By tailoring fire regimes to the needs of natural communities, managers can help restore and support the resilience of native species (Keeley et al. 2008; Pile et al. 2017b, 2019).

Prescribed fire is widely employed in the eastern USA as a key management tool, often in conjunction with tree thinning and herbicide application, to reduce fuel loads and enhance habitat conditions. This approach supports the regeneration of fire-adapted species such as pines and oaks while maintaining and restoring open-canopied, floristically diverse ecosystems, including longleaf pine forests and oak-hickory (*Carya* spp.) woodlands (Brose and Van Lear 1998; Van Lear et al. 2005; Dey et al. 2017). Additionally, these practices mitigate the effects of mesophication (Nowacki and Abrams 2008) by increasing understory light availability, improving conditions for seed germination and tree recruitment, and facilitating fuel accumulation that is necessary for frequent-fire ecosystems.

In fire-adapted ecosystems, the survival and composition of woody plant communities are strongly shaped by bark characteristics, particularly thickness (Lawes et al. 2013; Staver et al. 2020). Accounting for more than 20% of a tree's aboveground biomass, bark serves an essential role in nutrient storage, structural integrity, and protection of inner tissues (Rosell 2016; Neumann and Lawes 2021). Bark thickness, particularly as it relates to its thickness at the ground surface, is paramount for shielding the vascular cambium and sapwood from surface fire, with modest increases markedly enhancing a tree's survival and providing a significant evolutionary advantage (Michaletz et al. 2012). Although texture and moisture content also contribute to bark's insulating ability, thickness predominantly determines a tree's resistance to topkill (Lawes et al. 2013; Pausas 2017). Disproportionately thick basal bark at the expense of wood growth is a trait commonly associated with fire-tolerant trees (Shearman et al. 2018). Species adapted to regular surface fires tend to prioritize bark growth early on in structural development (Jackson et al. 1999; Pile et al. 2017a), and bark thickness in juvenile trees, when they are the most susceptible to fire damage, typically serves as a reliable predictor of their ability to withstand fire (Wang and Wangen 2011). Thus, thick bark is necessary for woody plant survival in fire-frequent ecosystems, making it a strong indicator of a species association with fire regime frequency and other community characteristics (Hoffmann et al. 2012).

For this study, we hypothesized that the bark thickness of invasive woody species would be more similar to that of native mesophytic species, thus offering significantly less protection from fire than the thicker-barked, native pyrophytic species. To test this hypothesis, we assessed bark thickness as a proxy of fire tolerance for six common woody invasive plants and compared them to the bark thickness of native species that are considered fire-tolerant (i.e., pyrophytic) and fire-intolerant (i.e., mesophytic) (Varner et al. 2016; Alexander et al. 2021). Moreover, as species adapted to frequent surface fires typically develop thick bark at the groundline (Graves et al. 2014; Hammond et al. 2015), and previous research has shown that a bark thickness of 5–10 mm is particularly effective for survival in such fire regimes (Harmon 1984), we further analyzed the relationship between bark thickness and tree size (diameter and height) to clarify patterns of early growth and fire protection. Given that bark thickness is primarily determined by evolutionary adaptation rather than by plastic responses to fire (Wang and Wangen 2011), our results can provide perspective on the facilitation of invasive species establishment and growth stemming from contemporary fire suppression practices and help guide management strategies for invasive woody plants in historically fire-frequent forests.

Methods

Study area

Trees for this study were collected in two locations, the Clemson Experimental Forest (34.6523 N, 82.8198 W) and Parris Island Marine Corps Recruit Depot (Parris Island MRCD, 32.3289 N, 80.6947 W), South Carolina, USA. The Clemson Experimental Forest is located in the upper Piedmont with elevations ranging from 180 to 275 m above sea level and characterized by mean temperatures ranging from 5.4 °C in January to 26.1 °C in July. The mean annual precipitation is 1372 mm. The major soil types include Ultisols, Entisols, and Inceptisols (USDA-NRCS 2015). The Clemson Experimental Forest includes over 7000 ha of forest area, including oak-dominated hardwood stands originating in the 1930 s and actively managed planted loblolly pine (*Pinus taeda*) forests. Parris Island MCRD is located on the Southeastern Coastal Plain with relatively flat topography ranging from 0 to 7 m above sea level and characterized by mild winters and hot summers and soils that are fine sands to fine loamy sands. Parris Island MCRD is 3257 ha, of which 608 ha are managed slash pine (*Pinus elliottii* Engelm.) plantations or mixed maritime forests. Both sites have variable fire use with histories of fire suppression.

Sampling design and data collection

Twelve woody species, six natives and six non-native invasives, were selected for inclusion in the study. Invasive trees and shrubs were selected based on their observed dominance (abundance and wide distribution) and were considered serious threats to native southern ecosystems by invasive plant councils and public agencies (Miller et al. 2004). The six invasive species are chinaberry (*Melia azedarach* L.), Chinese privet (*Ligustrum sinense* Lour.), Chinese tallow (*Triadica sebifera* [L.] Small), mimosa (*Albizia julibrissin* Durazz.), thorny-olive (*Elaeagnus pungens* Thunb.), and tree-of-heaven (*Ailanthus altissima* [Mill.] Swingle). Although there is inherent gradation when lumping species into broad dichotomous ecological trait groups (see Kreye et al. 2023 and Pile Knapp et al. 2024), for our purposes, we classified the six native species based on their presumed fire tolerance in southeastern USA ecosystems. Species considered fire-tolerant (pyrophytic) were black oak (*Quercus velutina* Lam.), mockernut hickory (*Carya tomentosa* [Lam.] Nutt.), and white oak (*Quercus alba* L.), and species considered fire-intolerant (mesophytic) were American beech (*Fagus grandifolia* Ehrh.), red maple, and yellow-poplar (*Liriodendron tulipifera* L.) (Shearman et al. 2018; Shearman and Varner 2021; Varner et al. 2021; Kreye et al. 2023).

We destructively sampled 300 individual stems across the two locations (Table 1). The sample size ranged from 16 to 35 stems per species. Most specimens were collected along county roads, forest roads, or areas of recent forest management (i.e., tree thinning) because most of these species tend to invade disturbed areas. We collected from a range of sites that varied in terms of the invasive species present, but we collected no more than five individuals per species at any given site.

Table 1 Basic information on the twelve sampled woody species selected for the study

Species	Common name	Abbreviation	Life form	Group	Sample size	Height (m; mean ± SD)	DBH (mm; mean ± SD)
Carya tomentosa	Mockernut hickory	MH	Tree	Pyrophytic	30	3.6 ± 1.5	23.6 ± 8.2
Quercus alba	White oak	WO	Tree	Pyrophytic	31	5.1 ± 2.4	32.8 ± 18.5
Quercus velutina	Black oak	BO	Tree	Pyrophytic	21	4.8 ± 2.5	28.2 ± 16.6
Acer rubrum	Red maple	RM	Tree	Mesophytic	33	5.0 ± 2.3	30.2 ± 16.4
Fagus grandifolia	American beech	AB	Tree	Mesophytic	30	4.9 ± 1.3	28.2 ± 10.7
Liriodendron tulipifera	Yellow-poplar	YP	Tree	Mesophytic	35	7.5 ± 2.8	38.3 ± 19.4
Ailanthus altissima	Tree-of-heaven	TH	Tree	Invasive	18	4.1 ± 1.9	40.9 ± 24.3
Albizia julibrissin	Mimosa	M	Tree	Invasive	20	5.9 ± 2.8	42.8 ± 19.0
Elaeagnus pungens	Thorny-olive	ST	Shrub	Invasive	17	3.6 ± 1.7	16.3 ± 6.3
Ligustrum sinense	Chinese privet	CP	Shrub	Invasive	22	4.6 ± 1.2	33.3 ± 14.7
Melia azedarach	Chinaberry	CB	Tree	Invasive	16	6.0 ± 2.7	56.0 ± 30.1
Triadica sebifera	Chinese tallow	CT	Tree	Invasive	27	8.3 ± 2.2	69.4 ± 23.4

Some species, particularly Chinese privet and thorny-olive, form clonal clumps, so we avoided cutting multiple stems from a single clump. Trees were cut down at ground level, and total tree heights were measured. Cross sections (or cookies) were cut along the length of the tree, cutting at 0.0, 0.3, 0.6, 0.9, and 1.4 m from ground level, with the north-facing side of the stem indicated on each cookie. Each cookie was individually labeled with a unique identification number, stored in labeled paper bags by tree number, and transported to the laboratory for further analysis. Samples were allowed to dry under ambient conditions in a temperature-regulated university building. Each cookie was sanded with either a belt or an orbital sander. The diameter and bark thickness of the cookies were measured by drawing three lines intersecting at 45-degree angles through the pith and measuring the outer part and the innermost part of the bark with a caliper. The measurement of bark thickness included the outer bark (rhytidome) and the inner bark (secondary phloem, phelloderm, and phellogen). The outer bark is the primary protective layer, but most studies on bark and fire report the combined thickness of the outer and inner bark (Shearman and Varner 2021).

Data analysis

Linear mixed-effects models (LMMs) were employed using the "lme4" package (Bates et al. 2015) to analyze three aspects: height-DBH relationships, absolute bark thickness (BT), and relative bark thickness (RBT) patterns across three groups (pyrophytic, mesophytic, and invasive species).

For height-DBH analysis, separate models were fitted for each group, with log-transformed height as the response variable and log-transformed DBH as the fixed effect predictor. Species was included as a random intercept effect (1|Species) to account for interspecific variation.

For bark thickness analyses, two response variables were examined: absolute bark thickness (BT, log-transformed) and relative bark thickness (RBT, logit-transformed due to its proportional nature). The RBT was calculated as the ratio of bark thickness to stem radius at the corresponding measurement height. Both models incorporated three-way interactions among DBH (absolute or standardized), group, and measurement height (0, 0.3, 0.6, 0.9, and 1.4 m) as fixed effects. To account for the hierarchical data structure, we included nested random effects: species-specific DBH responses (DBH|Species) and individual stem variations (1|Species:StemNum). DBH was standardized (mean-centered and scaled by one standard deviation) in the RBT model to facilitate effect size comparisons.

All models were fitted using restricted maximum likelihood (REML) estimation. Model performance was evaluated using conditional (total variance) and marginal (variance explained by fixed effects) R^2 values, calculated using the "MuMIn" package (Bartoń 2022). Model assumptions were verified using diagnostic plots from the "performance" package.

Post hoc analyses were conducted using the "emmeans" package (Lenth 2022) to examine the following: (1) group differences at three diameter classes (overall mean DBH ± 1SD), (2) pairwise comparisons among groups at each measurement height, and (3) slopes of DBH-bark thickness relationships across groups at different measurement heights. All pairwise comparisons were adjusted using Tukey's method ($\alpha = 0.05$). Model predictions and 95% confidence intervals were calculated using fixed effects while conditioning on random effects. Visualizations were created using the "ggplot2" package. All analyses were performed in R version 4.2.1 (R Core Team 2022).

Because two of the six invasive species are classified as shrubs (Table 1), not trees, we also analyzed and compared the results from all six invasive woody species and separately for the four invasive tree species. Both analyses yielded qualitatively the same results, and we reported only the results based on all six invasive species in the study.

Results

Allometric relationships between stem height and DBH across groups

Linear mixed-effects models demonstrated robust allometric relationships between stem height and DBH across all groups ($P < 0.001$ for all groups), with marginal R^2 values ranging from 0.706 to 0.779 (Fig. 1). Invasive species had a less steep slope in this relationship compared to mesophytic and pyrophytic species, indicating a slower increase in height per unit increase in DBH on the log–log scale (Fig. 1). Furthermore, the y-intercept for invasive species was higher than that for pyrophytic species, suggesting that invasive species start with a greater initial height (Fig. 1).

Interspecific variation in height-DBH relationships differed among groups, as indicated by the random effects structure. Mesophytic species showed the highest difference between conditional and marginal R^2 values (0.862 vs. 0.739), suggesting the largest species-specific variation. In contrast, pyrophytic and invasive species exhibited smaller differences between conditional and marginal R^2 values (0.825 vs. 0.779 and 0.768 vs. 0.706), indicating more consistent height-DBH relationships across species within the group (Fig. 1).

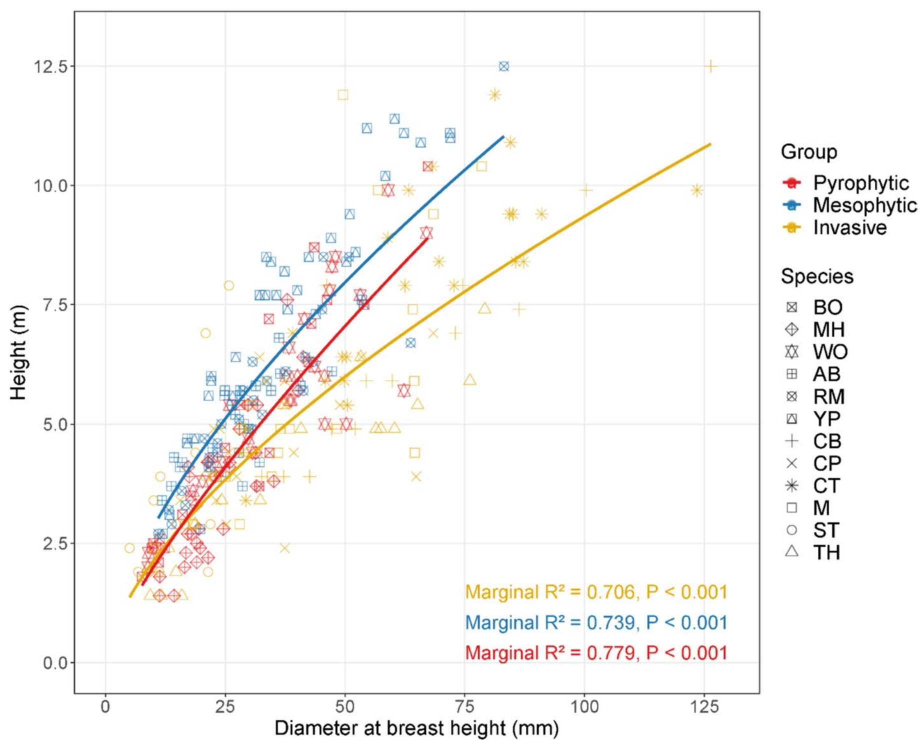

Fig. 1 Relationships between diameter at breast height (DBH) and stem height across groups. Points represent individuals of different species (shapes) and colors indicate groups (colors: red, pyrophytic; blue, mesophytic; yellow, invasive). Abbreviations: BO, *Quercus velutina*; MH, *Carya tomentosa*; WO, *Quercus alba*; AB, *Fagus grandifolia*; RM, *Acer rubrum*; YP, *Liriodendron tulipifera*; CB, *Melia azedarach*; CP, *Ligustrum sinense*; CT, *Triadica sebifera*; M, *Albizia julibrissin*; ST, *Elaeagnus pungens*; TH, *Ailanthus altissima*

Stem size effects on bark thickness patterns across fire-tolerance groups

Absolute bark thickness

Linear mixed-effects models revealed significant three-way interactions among DBH, group, and measurement height ($P<0.001$; Table 2). The models demonstrated high explanatory power, with a conditional R^2 of 0.921 and a marginal R^2 of 0.596.

Pyrophytic species consistently exhibited greater bark thickness compared to mesophytic and invasive species across all measurement heights (Fig. 2a). However, the differences in bark thickness between pyrophytic and the other two groups diminished with increasing measurement height (Fig. 2a). For example, at ground level (0 m), pyrophytic species had significantly thicker bark than mesophytic and invasive species ($P<0.001$), but at 1.4 m, the differences were marginally significant ($0.05<P<0.10$). No significant differences were found in bark thickness between mesophytic and invasive species at different measurement heights ($P>0.05$). The relationship between DBH and bark thickness varied significantly with measurement height and group (Fig. 3). Pyrophytic species exhibited progressively steeper slopes (log scale) with increasing measurement height, from 0.025 at ground level (0 m) to 0.040 at 1.4 m ($P<0.001$). In contrast, mesophytic and invasive species maintained similar slopes across measurement heights (at logit scale: approximately 0.025 and 0.020, respectively), with each fitted slope being significant ($P<0.05$). These results suggest that pyrophytic species exhibit a stronger vertical gradient in bark thickness compared to mesophytic and invasive species.

Relative bark thickness

Analysis of relative bark thickness revealed distinct patterns compared to absolute bark thickness. Significant effects of DBH ($P=0.023$), group ($P=0.015$), and their interaction with measurement height ($P<0.001$) were observed (Table 2). The model demonstrated high explanatory power, with a conditional R^2 of 0.870 and a marginal R^2 of 0.486.

Relative bark thickness decreased significantly with measurement height for pyrophytic species, whereas mesophytic and invasive species exhibited relatively stable patterns across measurement heights (Fig. 2b). Similar to bark thickness, the differences in relative bark thickness were most pronounced at ground level, with pyrophytic species showing significantly greater

Table 2 Summary of variance analysis (Type III ANOVA) for bark thickness and relative bark thickness models

Response variable	Source of variation	Sum Sq	Mean Sq	NumDF	DenDF	*F* value	*P* value
Bark thickness	DBH	7.901	7.901	1	4.95	149.207	< 0.001***
	Group	0.271	0.135	2	8.35	2.558	0.136
	Measurement height (MHT)	23.468	5.867	4	1176.00	110.803	< 0.001***
	DBH × Group	0.422	0.211	2	4.86	3.980	0.095
	DBH × MHT	2.879	0.720	4	1176.00	13.591	< 0.001***
	Group × MHT	5.499	0.687	8	1176.00	12.982	< 0.001***
	DBH × Group × MHT	2.234	0.279	8	1176.00	5.275	< 0.001***
Relative bark thickness	DBH (scaled)	0.524	0.524	1	6.73	8.652	0.023*
	Group	0.841	0.421	2	9.03	6.947	0.015*
	MHT	1.902	0.476	4	1176.00	7.857	< 0.001***
	DBH (scaled) × Group	0.168	0.084	2	6.46	1.387	0.315
	DBH (scaled) × MHT	1.844	0.461	4	1176.00	7.618	< 0.001***
	Group × MHT	5.022	0.628	8	1176.00	10.372	< 0.001***
	DBH (scaled) × Group × MHT	3.519	0.440	8	1176.00	7.268	< 0.001***

Notes:

Bark thickness: Conditional $R^2 = 0.921$; Marginal $R^2 = 0.596$

Relative bark thickness: Conditional $R^2 = 0.870$; Marginal $R^2 = 0.486$

Significance levels: *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$

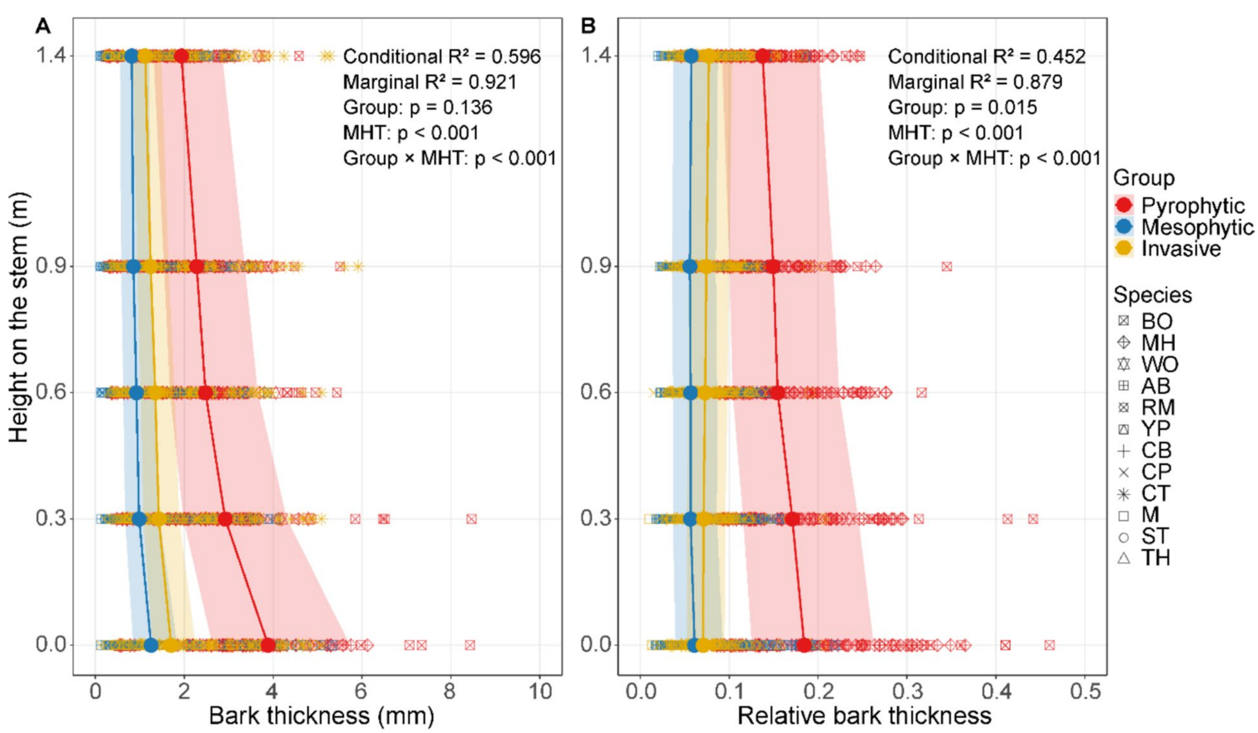

Fig. 2 Vertical variations in **A** bark thickness and **B** relative bark thickness among groups. Lines and shaded areas represent model predictions and 95% confidence intervals, respectively. Abbreviations: MHT, Measurement height; BO, *Quercus velutina*; MH, *Carya tomentosa*; WO, *Quercus alba*; AB, *Fagus grandifolia*; RM, *Acer rubrum*; YP, *Liriodendron tulipifera*; CB, *Melia azedarach*; CP, *Ligustrum sinense*; CT, *Triadica sebifera*; M, *Albizia julibrissin*; ST, *Elaeagnus pungens*; TH, *Ailanthus altissima*

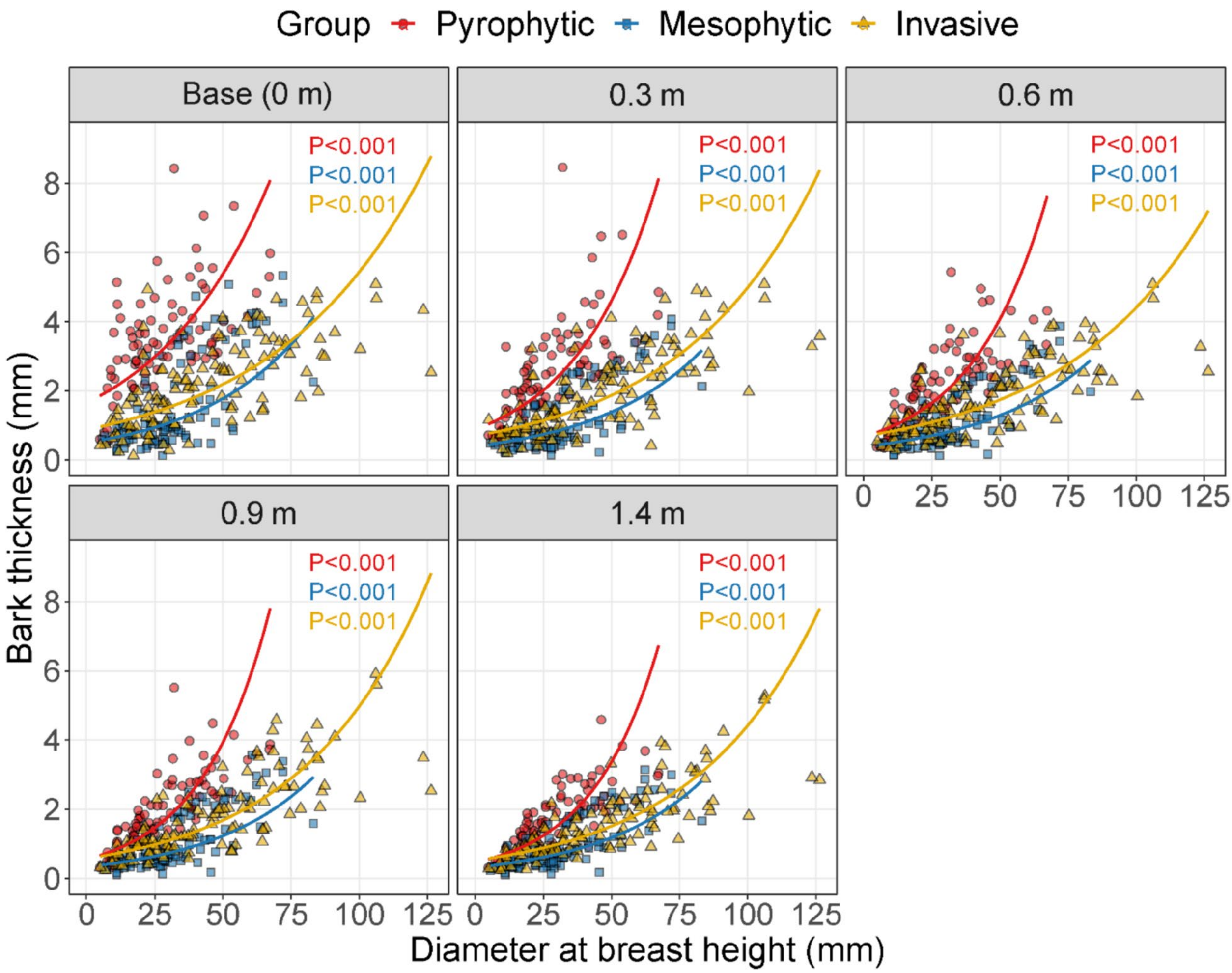

Fig. 3 Relationships between bark thickness and diameter at breast height (DBH) across different stem heights for species groups. For each panel, the x-axis represents the DBH of individual trees, which serves as a reference point for all bark thickness measurements at multiple stem heights (i.e., each vertical profile). The y-axis in each panel shows the bark thickness measured at the indicated height along the stem

relative bark thickness compared to both mesophytic and invasive species ($P < 0.01$). These differences diminished at higher positions, suggesting that enhanced bark allocation at the base of the stem in pyrophytic species is particularly crucial during early developmental stages (Fig. 2b). There were also no significant differences in relative bark thickness between mesophytic and invasive species at different measurement heights ($P > 0.05$). For pyrophytic species, the relationship between DBH and relative bark thickness transitioned from negative at ground level (slope, − 0.282 at logit scale; $P < 0.001$) to values near zero or positive at higher positions (slopes at logit scale, − 0.001 to 0.118; $P > 0.05$), although the slopes were only significantly different from zero at ground level (Fig. 4). Conversely, mesophytic (slopes at logit scale, − 0.171 to − 0.090) and invasive (slopes at logit scale, − 0.109 to − 0.059) species maintained relatively stable negative relationships across all measurement heights, with trends that were not always statistically significant (Fig. 4).

Discussion

Woody invasive plants are a significant management challenge in the eastern USA. Many ecosystems within this region, particularly in the southeastern USA, have developed with frequent fire as a determinant of the structure and composition of the community. Fire suppression policies at the turn of the nineteenth century occurred as many invasive plants were starting to get a strong foothold by escaping ornamental plantings and naturalizing in the south. For example, tree-of-heaven, Chinese tallow, chinaberry, and mimosa were all introduced in the late 1700 s (Waggy 2009; Pile et al. 2017c; Weber 2017; Huebner and Wickert 2024). Chinese privet was introduced in 1852 and thorny-olive in 1830 (Dirr 1983; Gucker 2011). Most of these species

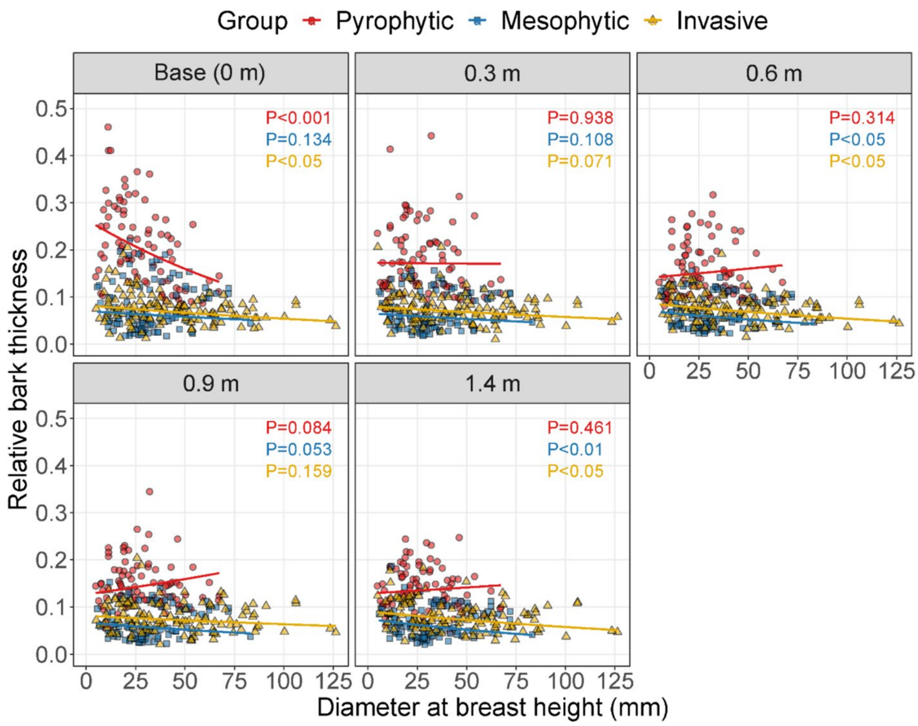

Fig. 4 Relationships between relative bark thickness (ratio of bark thickness to stem radius) and diameter at breast height (DBH) across different stem heights for species groups. For each panel, the x-axis represents the DBH of individual trees, which serves as a reference point for all bark thickness measurements at multiple stem heights (i.e., each vertical profile). The y-axis in each panel shows the bark thickness measured at the indicated height along the stem

were documented as spreading from cultivation by the early to mid-nineteenth century (Small 1933; Duncan 1950). Woody invasive plants possess many traits that aid in their success, including tradeoffs in resource allocation. We suspected that changes to historic frequent fire regimes likely contributed to their success as fire suppression is also attributed to increases in the abundances of native mesophytic species. Further, ecological communities that have maintained their historic frequent fire regime through time, such as some relict longleaf pine systems, may be some of the least invaded by woody species (Simberloff 2001). Although our study does not directly address the relationship between fire suppression and invasion, our destructive sampling and analysis demonstrated that common woody invaders of southeastern forests have bark thickness traits similar to those of native mesophytic species. Specifically, both groups allocate less biomass to bark, especially at the ground surface, where bark offers the most protection during surface fires. We also determined that invasive species prioritize early height growth over diameter growth. These findings have important implications for invasive plant control and natural community management.

Relationships between DBH and height

The three groups exhibited different growth strategies. For a given stem diameter, invasive species tend to be taller than pyrophytic species when height was less than 2.8 m, reflecting greater investment in height growth during early development. This is likely due to the selected pyrophytic species being larger, both in terms of size and height, and longer lived than the predominately short-lived, shorter-statured, at maturity, invasive species. This has implications when these species are in direct competition: invasive species may outcompete native pyrophytic species early on by gaining better access to light, but pyrophytic species may dominate in long-term successional competition with woody invasive plants. For example, Pile et al. (2019) compared the growth dynamics of invasive Chinese tallow with native species such as slash pine and sweetgum (*Liquidambar styraciflua* L.), noting that the rapid early growth of Chinese tallow does not offset its earlier onset of growth decline and senescence as slash pine and sweetgum continue to grow in height and diameter. The lack of height growth priority, especially when < 2.8 m tall, for pyrophytic species is likely a tradeoff due to the resources demanded for bark growth and other compensatory strategies to reduce the impacts from topkill, such as prioritizing root growth. Mesophytic species had greater variability in their relationship between early height and diameter growth, likely due to the differences in the species we selected. Yellow-poplar is a fast-growing, shade-intolerant species with a large stature. In comparison, red maple and American beech are slower-growing and shade-tolerant species. Our findings help support other work suggesting that successional dynamics may favor native species over the long run (Flory et al. 2017; Link et al. 2019), especially with active intervention (e.g., release of desired species) during key developmental stages (Pile et al. 2019).

Influence of stem size on bark thickness

Thick bark is one adaptive trait associated with fire tolerance in ecosystems characterized by frequent surface fires (Keeley et al. 2011; Pausas 2015). Previous research on bark thickness has often focused on measurements at a single height, which may not accurately reflect the variability in bark thickness among species (Graves et al. 2014). In our study, although pyrophytic and invasive species had comparable bark thickness at breast height, at the ground line, the bark thickness of pyrophytic species was 2.3 times higher than that of invasive species. Pyrophytic species allocated around 20% of their ground line diameter to bark thickness, while mesophytic and invasive species allocated less than 10%. The absolute bark thickness of all species exhibited a decreasing trend with increasing height, yet pyrophytic species demonstrated a more pronounced decline from ground line to breast height. Supporting our hypothesis, the distribution of bark along the stem between mesophytic and invasive species was similar suggesting that invasive species do not prioritize the allocation of resources to thick bark near the surface of the ground.

We further investigated the relationship between stem size (DBH) and bark thickness to assess the potential impact of surface fires on different species groups across size gradients, given that bark thickness is strongly correlated with stem diameter. As anticipated, larger stems had significantly thicker bark than smaller stems. The bark thickness of pyrophytic species was significantly greater than the other two groups, with the bark thickness of invasive species falling between pyrophytic and mesophytic species, but more similar to mesophytic species. Notably, the relative ground line bark thickness of pyrophytic species declined steeply with increasing diameter, reflecting prioritization of bark investment during early developmental stages. In contrast, mesophytic and invasive species showed minimal Changes in relative bark thickness with diameter growth. Previous research has suggested that stem diameter explains 72% of the total variation in bark thickness, meaning that relatively little variation is left to be explained by environmental factors (Rosell 2016). In ecosystems where fires are rare, some variability in bark thickness is still observed, likely driven by other factors (Pausas 2015; Nolan et al. 2020; Tuo et al. 2021). Our study found that regardless of the horizontal (DBH) and vertical (height) gradients, pyrophytic species differ from the other two (mesophytic and invasive) groups, with the bark characteristics of invasive species being similar to those of mesophytic species. Therefore, bark thickness indicates the core differences between the pyrophytic species and the other two groups.

Implications for management

Extensive research has established that fire-tolerant species exhibit thicker bark than their fire-sensitive counterparts, enhancing their survival in ecosystems subject to frequent, low-intensity fires (Pausas 2015). Fire-intolerant species, such as red maple and American beech, have had dramatic increases in their abundance across eastern USA forests, with fire suppression and departure from historic fire regimes likely major contributors (Abrams 1998; Fei and Steiner 2007). In our study, the congruence in absolute and relative bark thickness patterns between mesophytic and invasive groups suggests that prescribed fires could be employed to manage invasive species similarly to mesophytic species. However, mesophytic species such as red maple and American beech are challenging to manage with fire alone because they have strong resprouting ability (Green et al. 2010; Izbicki et al. 2020), and woody invasive plants are also aggressive resprouters (Pile Knapp et al. 2024). Although it seems feasible to use prescribed fire to manage these six invasive species, eliminating them may still be difficult, due to their vigorous capacity to resprout. Management that includes repeated fire and herbicide may be effective for reducing invasive species populations and maintaining them at juvenile life stages (Pile et al. 2017c; Rebbeck et al. 2019; Fan et al. 2021). Further, native pyrophytic species are uniquely adapted to frequent surface fire regimes, and repeated fire is necessary for the development of open forest ecosystems (Pile Knapp et al. 2024).

Invasive species are notably competitive, primarily due to their rapid early growth rates and aggressive resprouting following topkill (Nolan et al. 2020). These traits imply that despite topkill with frequent surface fires due to their thinner bark—similar to mesophytic species—their ability to resprout equips them to survive once established. However, targeting woody invasive plant populations with repeated prescribed fire when they are young and immature may increase long-term control (Fan et al. 2021). Repeated topkill depletes root carbohydrate reserves, thereby diminishing subsequent resprout vigor (Bond and Midgley 2003; Sakai and Sakai 1998). Consequently, further research is needed to quantify the resprouting capacity of many invasive species following multiple disturbances, such as repeated prescribed fires, especially under different canopy densities or seasons. For example, topkill may be more effective at reducing sprouting capacity when residual canopy density is high (Luken and Mattimiro 1991) or when conducted during the growing season (Richburg 2005).

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Authors' contributions
DL made substantial contributions to the formal analysis and writing of the manuscript. LPK made substantial contributions to the data curation, methodology, and writing of the manuscript. BB made substantial contributions to the data collection, formal analysis, and writing of the manuscript. TS made substantial contributions to the formal analysis and writing of the manuscript. CS, CA, and HS made substantial contributions to the data collection, data curation, and writing of the manuscript. GGW made substantial contributions to the conceptualization, funding acquisition, methodology, project administration, and writing of the manuscript. All authors have read and approved the manuscript.

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Data availability
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

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