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PERSPECTIVE

Longleaf pine savannas reveal biases in current understanding of savanna biogeography

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Abstract

Biased understanding of savanna biogeography: Grasslands and savannas exist across a wide range of climates. Mesic savannas, with highly variable tree densities, are particularly misunderstood and understudied in comparison to arid and semi-arid savannas. North America contains historically extensive mesic savannas dominated by longleaf pine. Longleaf pine savannas may have once been the largest savanna type on North America, yet these ecosystems have been overlooked in global syntheses. Excluding these "Forgotten Ecosystems" from global syntheses biases our understanding of savanna biogeography and distribution.

Evolutionary history and distinct climate of longleaf savannas: We assessed the evolutionary history and biogeography of longleaf pine savannas. We then harmonize plot data from longleaf savannas with plot data from valuable existing global synthesis of savannas on other continents. We show that longleaf pine savannas occur in a strikingly distinct climate space compared to savannas on Africa, Australia, and South America, and are unique in having wide ranging tree basal areas.

Future directions: Grass-dominated ecosystems are increasingly recognized as being ancient and biologically diverse, yet threatened and undervalued. A new synthesis of savanna ecosystems considering their full range of distributions is needed to understand their ecology and conservation status. Interestingly, the closest analogues to North American savannas and their relatives in Mesoamerica and the Caribbean may be Asian savannas, which also contain mesic fire-driven pine savannas and have been similarly neglected in existing global syntheses.

KEYWORDS
Aristida, Mesic savanna, north American grasslands, north American grasslands conservation act, *Pinus palustris*, savanna, wiregrass

1 | BACKGROUND

Strömberg and Staver (2022) recently argued that among undervalued and under threat grassy biomes, mesic savannas in particular are misperceived. Whereas arid to semiarid grasslands and savannas are well recognized as natural habitats, mesic savannas are often viewed as degraded forest because their tree densities are highly variable (Ratnam et al., 2011; Strömberg & Staver, 2022). This makes them vulnerable to misclassification as forest and to ecologically inappropriate tree planting as a climate change mitigation strategy (Griffith et al., 2017; Veldman et al., 2019).

Large regions of North America are dominated by grasses (Figure 1). Within the range of grassy biomes in North America, the North American Coastal Plain (NACP) is one region that is classified as a mesic grassy biome (Strömberg & Staver, 2022). The longleaf pine savannas of North America span the NACP and are

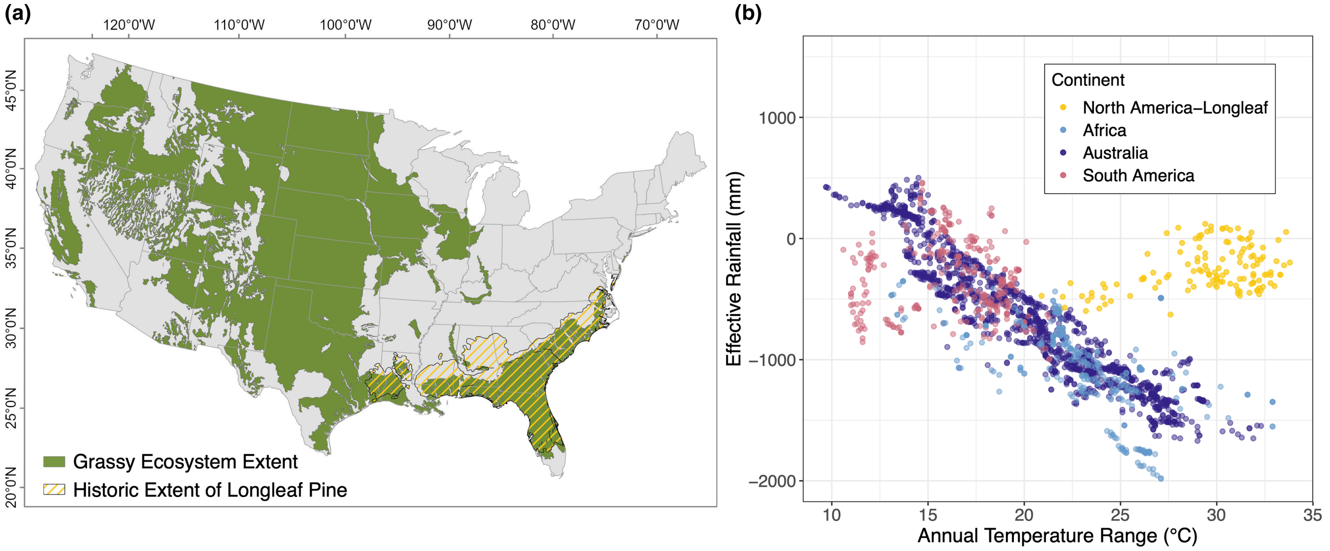

FIGURE 1 Longleaf pine savannas may have been the largest savanna type in North America and their evolutionary history suggests that they should be included as part of the tropical grassy biome (a). Longleaf pine savannas occur in a distinct climate space compared to savannas on other continents (b). Grassy ecosystem extent from Griffith et al. (2020) and longleaf pine historical extent from https://figshare.com/articles/dataset/SE_pine_savannas_woodlands_zip/6828848. Although we show the full range of longleaf pine habitats, only regions of fire-driven longleaf pine dominated communities (i.e., savannas with C_4 understory) from (a) were included in (b). Data from tropical savannas on Africa, Australia, and South America from Lehmann et al. (2014).

among the ecosystems that have been called "Forgotten Grasslands" (Noss, 2012) because awareness that they are naturally dominated by grasses is limited. Historically, longleaf pine savannas may have been one of the most extensive grassy ecosystems in North America covering approximately 37 million hectares of the land area (Figure 1) (Frost, 2007; Nuzzo, 1986). By some estimates, conversion to agriculture, fire suppression, and other human activities have reduced longleaf pine savannas by at least 96% of their original range (Frost, 2007; Noss et al., 2015).

Although named after the dominant tree species, longleaf pine (*Pinus palustris*), nearly all of the biodiversity occurs in the high-light environment of the grassy understory. The maintenance of open canopy conditions is created by gap dynamics and fire-inhibiting hardwood encroachment (Glitzenstein et al., 1995; Mcguire et al., 2001; Myers & Van Lear, 1998; Platt, 1988). The high frequency of low-intensity fires in longleaf pine habitats is in part due to the flammability of grasses with the C_4 photosynthetic pathway such as wiregrass and bluestems (*Aristida* spp. and *Andropogon* spp., respectively) (Fill et al., 2016; Wenk et al., 2011). Indeed, a key distinction between longleaf pine savannas and contemporary eastern U.S. temperate forests is the ecosystem function associated with fire and C_4 grasses in longleaf pine savannas (Griffith et al., 2015). These ecosystems are also exceptionally biodiverse: frequently burned longleaf pine savannas can have as many as 52 plant species in a square meter, which ranks among the highest in the world at fine scales and is the highest in North America (Walker & Peet, 1984; Wilson et al., 2012).

Mesic savannas of North America have thus been a blindspot in global and North American grassland ecology and conservation, biasing our broader understanding of savanna biogeography and distribution. The determinants of savanna distribution, structure, and function are an active area of research but North America has not been included in several pioneering and valuable global syntheses due to the tropical focus of these studies (e.g., (Lehmann et al., 2014; Pennington et al., 2018; Staver et al., 2011)). Tree density and growth are highly variable in savannas, and sensitive to factors such as climate, soils, and disturbance regimes. Research across Africa, Australia, and South America has identified rainfall and rainfall seasonality as critical to understanding savanna structure and function, either through direct effects of limiting tree growth or indirect effects on tree growth through fire (Lehmann et al., 2011; Lloyd et al., 2008; Sankaran et al., 2005; Staver et al., 2011). While these common drivers of savanna structure and function have emerged, there are key biogeographic differences related to interactions among species' traits, soil fertility, historical contingency, and other factors (Hoffmann et al., 2012). Here, we examine the biogeography of North American longleaf pine savannas in a global context by reviewing their evolutionary history and contrasting their distribution, structure, and function with savannas on other continents.

2 | BIOGEOGRAPHIC AND EVOLUTIONARY HISTORY OF MESIC LONGLEAF PINE SAVANNAS

The southeastern region of North America is the centre of diversity for both longleaf pine and wiregrass clades, and longleaf pine and wiregrass exhibit almost identical geographic ranges. The evolutionary history of both longleaf pine and wiregrass suggests this extensive North American savanna evolved independently, separate from other grassy ecosystems on North America and other continents.

But, the timing of this ecosystem's appearance generally coincides with the global dominance of C_4 grasslands during the late-Miocene to early-Pliocene (Cerros-Tlatilpa et al., 2011; Edwards et al., 2010). Globally, grassy ecosystems are dominated by only a few grass lineages: Chloridoideae, Andropogoneae, and Pooideae (Griffith et al., 2020; Strömberg & McInerney, 2011). The wiregrass genus, *Aristida*, within the Aristidoideae subfamily, is a large genus with four centres of diversity globally, including a core North American clade. The *Aristida* clade in North America, mostly species in the southern U.S., dates to the Pliocene, approximately 4.81 Mya (Cerros-Tlatilpa et al., 2011). C_4 ecosystems dominated South America before North America, but the *Aristida* clade in South America is younger than the North American clade (2.37 Mya; Cerros-Tlatilpa et al., 2011). Evidence from the central Great Plains region of North America also shows a shift to C_4 dominance around the late Miocene-early Pliocene, but not by the Aristidoideae lineage (Strömberg & McInerney, 2011). While continental differences in the rise of distinct C_4 lineages and their associated traits have been acknowledged (Edwards et al., 2010; Strömberg & Staver, 2022), even in the Americas the generally synchronous spread of C_4 ecosystems occurred in disparate hotspots, with *Aristida* being a unique lineage among other dominant C_4 grasses.

Longleaf pine is closely related to tropical pines in the Greater Antilles and Central America. The longleaf clade (*Australes* subsection of the *Pinus* genus) radiated from the southeast of North America into the Florida Peninsula and the Greater Antilles. A common North American *Pinus* ancestor likely split into two lineages about 15 mya during the Miocene – the clade that includes longleaf pine and a sister clade in Mexico and Central America (Gernandt et al., 2018; Jin et al., 2021). Longleaf pine is a “fire tolerator” with a suite of adaptations to withstand frequent fire, including a unique grass stage (Keeley, 2012). Many *Pinus* species closely related to longleaf pine, of which three are tropical, have fire-adapted traits (Table 1). Many of these closely related tropical pine ecosystems are fire-suppressed, but select studies have shown post-fire flowering response of understory species and high understory species richness in fire-maintained open-canopy sites (Myers & Rodríguez-Trejo, 2009). This evolutionary history shows that the longleaf pine ecosystem is closely related and ecologically similar to fire-dependent tropical pine savannas. Other regions with fire-dependent tropical pine savannas occur throughout Asia – East Asia, South Asia, and Southeast Asia – and historically may have been more widespread in these regions (Myers & Rodríguez-Trejo, 2009; Ratnam et al., 2016).

TABLE 1 *Pinus* species from the Australes clade (Gernandt et al., 2018) and fire-adapted traits.

Species	Geographic distribution	Fire traits
P. palustris	Southern United States	RE, GS, RS (seedlings), FIG (after GS), BPS, RH, TB, SP, RCS
P. echinata	Southern United States	RE, RS, TB, RCS
P. elliottii var. *elliottii*	Southern United States	RE, FIG, TB, SP, RCS
P. elliottii var. *densa*	Southern United States	RE, GS[d], TB, SP, RCS
P. glabra	Southern United States	FIG[e], BPS, RH, TB[f]
P. pungens	Southern United States	RE, RS, BPS, RH, TB, SP
P. rigida	Southern United States	SC, RE, RS, TB
P. serotina	Southern United States	SC, RE, RS, TB, SP, RCS
P. taeda	Southern United States	RE, RS (seedlings), TB, SP, RCS
P. occidentalis	Hispanola	RE, TB, SP
P. caribaea[g]	Cuba, Isla de la Juventud, Bahamas, Central America	RE, RS, TB, SP, RCS
P. cubensis	Cuba	RE, TB, SP

Note: Traits from Myers and Rodriguez-Trejo (Myers & Rodríguez-Trejo, 2009) except for *P. glabra*[a] and *P. pungens*[bc]

Abbreviations: BPS, buds protected with scales; FIG, fast initial growth; GS, grass stage; RCS, recovery from crown scorch; RE, regenerates in fire-created bed; RH, rooting habit; RS, resprout; SC, serotinous cones; SP, self-pruning capacity; TB, thick bark, high crown.

[a] https://www.fs.usda.gov/database/feis/plants/tree/pingla/all.html.

[b] https://www.fs.usda.gov/database/feis/plants/tree/pinpun/all.html.

[c] Weakley, A. S. (2022). Flora of the southeastern United States. University of North Carolina at Chapel Hill Herbarium (NCU).

[d] *P. elliottii* has an early slow growth stage, which some do not consider a true grass stage.

[e] In disturbed sites, such as after an extreme wildfire or hurricane.

[f] Thick bark is produced on the lower part of old trees.

[g] There are three varieties of *P. caribaea* (var. *caribaea*, var. *bahamensis*, and var. *hondurensis*) but trait data could not be found for each.

3 | THE UNIQUE CLIMATE AND STRUCTURE OF LONGLEAF PINE SAVANNAS

We examined the climate space of longleaf pine savannas by extracting mean annual temperature (MAT), mean annual precipitation (MAP), mean annual temperature range, precipitation seasonality, and effective rainfall (potential evapotranspiration subtracted from mean annual precipitation) from the known geographic range of longleaf pine with C_4 grass understory (see Methods in Supporting Information). Compared to tropical savannas on Africa, Australia, and South America, longleaf pine savannas occur in distinct climates (Figure 1). Longleaf pine savannas experience a much larger range in temperature yet occur in more narrow limits of effective rainfall, a measure of plant available moisture. In terms of MAP, savannas in Australia and South America can occur in wetter regions than longleaf pine savannas, while African savannas can occur in drier regions than longleaf pine savannas (Lehmann et al., 2011; Strömberg & Staver, 2022). Most notably, longleaf pine savannas occur in regions with less seasonality in rainfall compared to tropical savannas on other continents (see Figure S1 in Supporting Information). Because seasonal drought is considered a necessary condition for fire in other tropical savanna regions, the role of plant traits, such as the flammability of wiregrass and longleaf pine's long needles, help explain convergent fire regimes in climatically dissimilar regions (Archibald et al., 2018; Fill et al., 2012; Platt et al., 2016; Simpson et al., 2022).

In addition to a unique floristic composition and associated plant traits, in the southeast U.S., the relationship between rainfall seasonality and fire follows a unique casual sequence that is dependent on lightning. In general, wet summers promote vegetation growth and fuel accumulation. During the following winter, these fuels begin to cure so that by the end of winter and early in the spring when the lightning season begins, cured fuels in combination with a high rate of lightning strikes promote fires (Fill et al., 2016; Noss, 2018). Interestingly, Fill et al. (2016) show that *Aristida*, which is generally rare as a dominant grass in savanna regions, is highly flammable even under moist conditions. In tropical regions that experience convective storms during the dry to wet season transition, lightning fires may be more common than currently realized (Myers & Rodríguez-Trejo, 2009). Current thinking about savanna pyromes is focused on seasonal drought, for example, tropical dry season fuel curing and ignition, whereas other factors may be more important in mesic savannas. Longleaf pine ecosystems highlight unique relationships between climate and fire, which may be characteristic of other mesic savannas.

Using plot data from 567 longleaf pine-dominated sites spanning the range of longleaf pine-wiregrass savannas in the southeastern U.S., we tested alternative hypotheses for how fire, soils, and climate affect tree (i.e., longleaf) basal area building on the important work of Lehmann et al. (2014). The best-fit models (lowest Bayes Information Criterion) show that moisture availability and seasonality are key drivers of longleaf pine tree basal area (see Table S1, S2, and Figure S2 and Methods in Supporting Information). While these are the same determinants of tree basal area consistently identified in other tropical savannas (e.g., Lehmann et al., 2014; Sankaran et al., 2005; Staver et al., 2011), the unique biogeographic histories on different continents result in savanna vegetation with unique fire and climatic responses (Lehmann et al., 2014).

Longleaf pine savannas are unique in having wide ranging basal areas compared to other tropical savannas (see Figure S1 in Supporting Information). This appears in part because of the divergent responses of recruitment and growth to fire at different sites. Fire is thought to reduce tree basal area in other tropical savannas (Lehmann et al., 2014). However, we show that relationships with fire may depend on stand structure. In plots with high tree basal area, basal area decreases with higher fire frequency and there is slower recruitment of additional stems (see Figure S3 in Supporting Information). In plots with low tree basal area, basal area appears to increase with higher fire frequency, and the increase in basal area is associated with the recruitment of many new individuals. Longleaf pine recruitment and seed germination can benefit from frequent fire and exposed bare mineral soil (Grace & Platt, 1995; Mcguire et al., 2001; Platt, 1988). One key factor is the spatial patchiness of fires, which can result in regeneration patches for longleaf juveniles (Robertson & Platt, 2019). Longleaf pine growth rates can also increase with higher fire frequencies, depending on interactions with temperature and precipitation (Zampieri & Pau, 2022). While longleaf pine savannas are generally considered mesic compared to other grassy biomes globally (Strömberg & Staver, 2022), there are distinct longleaf pine communities, from xeric to hydric, that differ in their soils and climate. These communities have variable tree densities (Zampieri & Pau, 2022), which may be associated with different responses to fire.

4 | A NEW SYNTHESIS OF TROPICAL GRASSY BIOMES IS NEEDED

Limited awareness of the distribution of grassy ecosystems remains a persistent challenge (Griffith et al., 2017; Veldman et al., 2019). The unique evolutionary history, climate, plant traits, and ecological function of longleaf pine savannas highlight both their global importance and the diversity of grassy ecosystems that is often overlooked across North America. Because grassy biomes exist over a wide range of climates (Strömberg & Staver, 2022), a critical gap in our understanding of tropical grassy biomes is whether mesic savannas, with higher tree densities, are functionally distinct from more commonly studied arid and semi-arid savannas.

Interestingly, the closest analogues to longleaf pine savannas outside of close relatives in Mesoamerica and the Caribbean may be C_4 grass-dominated fire-dependent Asian pine savannas (Ratnam et al., 2016), which have similarly been left out of global scale syntheses. Asian savannas, similar to longleaf pine savannas, can have relatively high tree densities, which led to its misclassification as forest by colonists who imposed extractive uses such as timber harvesting and fire exclusion (Ratnam et al., 2016). In fire-suppressed habitats, Asian pine savannas are often invaded by *Quercus* spp. (Ratnam et al., 2016), similar to fire-suppressed longleaf pine savannas (Platt, 1988). As Ratnam et al. (2016) have described, some *Pinus* species in Asian pine savannas exhibit a grass stage like longleaf pine, among other fire adaptation traits. Asian pine savannas also occur over a large rainfall gradient (mean annual precipitation 900–3200 mm), with relatively cooler temperatures, and may have slower tree growth rates due to nutrient poor soils, similar to longleaf pine (Ratnam et al., 2016).

We suggest that future syntheses focus on the ecological function of the grassy understory component in addition to differences in tree basal area, as a focus on tree basal area alone contributes to the misunderstanding of mesic savannas. Consideration of old-growth characteristics, for example, species-rich understory, dominance of long-lived perennials, and diversity of belowground structures, can help characterize the full complexity of grassland structure and function over the long-term (Buisson et al., 2022; Peet et al., 2018; Veldman et al., 2015). In North America, our opportunity to understand the ecology and diversity of grassy ecosystems is threatened by their increasingly imperilled status.

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CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

All data used in analyses are publicly accessible and cited in the main text.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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