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ARTICLE

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Locating potential historical fire-maintained grasslands of the eastern United States based on topography and wind speed

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Abstract

Historically, grasslands with limited tree presence were embedded in a matrix of predominantly open oak and pine forests in the eastern United States. These open ecosystems mostly have been lost to other land uses, particularly agriculture, and also to closed forests under fire exclusion because frequent surface fire prevents tree encroachment. We located the potential extent of eastern fire-maintained grasslands by applying the random forests and C5.0 classifiers to determine the relationship between mapped areas of historical grasslands and topography and wind speed, which are proxies for surface fire frequency. A generalized ruleset was that fire-maintained grasslands occurred at roughness values of less than 95, or flatter sites, and wind speeds ≥3.4 m s^{-1}, which created large fire compartments. Potential grasslands covered 27 million ha, or 14% of the 200 million ha of the eastern United States, although these fire-maintained locations also may have been savannas or open woodlands historically. Currently, potential grassland locations are 40% crops, 25% pasture, 18% forests, and 13% developed land, with about 1.5% each of herbaceous upland vegetation, herbaceous wetlands, and shrublands. According to historical accounts, fire-maintained grasslands generally transitioned to dense young tree growth within a 20-year interval after fire exclusion; in Kentucky, the transition transpired during the periods 1790–1810 or 1810–1830, but dates vary with Euro-American settlement time. Finding the forgotten grasslands of the eastern United States, with this mechanistic approach to estimate fire disturbance, is an important first step for recovering and managing eastern grassland biodiversity.

KEYWORDS
climate, edaphic, fire, land use, prairie, savanna, woodland

INTRODUCTION

Historically, abundant grasslands and open oak and pine forests of the eastern United States largely have disappeared from current landscapes, which instead are dominated by closed forests, agriculture, or other land uses (Hanberry, Bragg, & Hutchinson, 2018; Noss, 2013). Grasslands may be defined as ecosystems within which plant cover or biomass, and usually species richness, is concentrated in a graminoid-dominated herbaceous layer (Frost, 1998; Noss, 2013). A divide exists between grasslands and closed forests, which do not contain a dense herbaceous layer, but such herbaceous layers occur in grasslands, savannas, open woodlands, and closed woodlands, along a continuum of increasing tree densities. Savannas represent the intermediate phase of the continuum between treeless grasslands and open woodlands. Because woodlands often surrounded grasslands in the eastern United States, most eastern grasslands may have been inextricable from savannas. For example, historical accounts documented small, stunted trees and tree groves in grasslands that increased within a few decades after Euro-American settlement (Gleason, 1922).

Eastern grasslands and open forests occur in a humid climate with seasonal precipitation and range across precipitation and temperature gradients in most of the eastern United States, albeit excluding some of the northernmost parts of the northern states. Therefore, climate has not been attributed as a reason for existence of eastern grasslands in the same manner that climate has been used to explain large well-differentiated grassland regions, such as the Great Plains region of central North America, which occurs along a precipitation gradient between forests and shrubland regions (Hanberry, 2021; Transeau, 1935). Indeed, the specific climatic factors that may maintain the Great Plains grasslands have not been isolated and it would be even more challenging to pinpoint fine-textured (micro)climates that separate grasslands from surrounding forests in the eastern United States.

Likewise, most soils can support both herbaceous plants and trees. Eastern grasslands occur on every soil order, although mollisols, which are often associated with grasslands, have limited distribution in the eastern United States. Therefore, soils in general have weak associations with both fire frequency and vegetation type throughout most of this region. Exceptions include localized glades that have a "hydroxeric" (i.e., annual variation from very wet to very dry) microclimate, which is determined largely by edaphic factors, typically shallow soils; in addition, the soils of some barrens and glades are inimical to tree growth due to toxicity from heavy metals or low effective moisture levels (Noss, 2013; Tyndall & Hull, 1999). Whereas some serpentine barrens in eastern North America contain largely treeless vegetation in the absence of fire, most require periodic fire (Tyndall & Hull, 1999).

Surface fire is the mechanism that provides the most consistent explanation for historical abundance of grasslands and open forests in the eastern United States, which has moderate precipitation sufficient to sustain the alternative state of closed forests (Hanberry, Abrams, & White, 2018; Noss, 2013). This explanation, incorporating pronounced wet and dry seasons, holds for all the major savanna regions of the world (Bond, 2019; Bond et al., 2005; Staver et al., 2011). The abundance of eastern grasslands increased with fire frequency both in the Southeast, where precipitation was greatest, and in the western border with the drier Great Plains grasslands of central North America. In the eastern United States, fire favors herbaceous vegetation and low-density fire-tolerant oak and pine species over fire-sensitive tree species; therefore, conditions that maintain most grasslands also may support open forests and closed forests under different fire regimes. Savannas and woodlands of longleaf pine (*Pinus palustris*) and other southern pines that historically dominated the relatively flat southeastern US Coastal Plain (Wahlenberg, 1946) require very frequent fire, up to every 1–3 years depending on site factors and landscape context, to protect the grassland component against tree encroachment (Noss, 2018).

Historical accounts, conceptual publications, and recent research have indicated that most North American grasslands may exist under frequent surface fire augmented by strong westerly winds and flat topography, which produce large fire compartments, that is, the area burned by an unrestricted fire (Christy, 1892; Hanberry, 2021; Harper, 1911). All else being equal, fire frequency increases with size of the fire compartment, which is determined in large part by topography and increased by wind speed (Frost, 2006). Ross (1882, p. 214) witnessed spreading fire in the extensive grasslands at the border of Tennessee and Kentucky: "During the winter [1812–1813] I first saw the tremendous fires caused by the burning of the dry grass. In many places, this grass was very thick and tall; and when perfectly dry, should it get on fire, the wind being high, the spectacle became truly sublime, especially at night… The flames, when the wind blew strong, would move with such rapidity that animals of all kinds had to hurry forward to avoid perishing in them." The number of fire ignitions can both be increased and be decreased by humans; fire was a management tool used by indigenous humans to maintain biodiverse grasslands and open forests and initially applied by Euro-American settlers.

Nevertheless, not all grasslands are dependent primarily on relatively frequent fire to remove trees or on harsh soils to suppress tree establishment. Poor-quality sites have low productivity, resulting in delayed and disrupted tree establishment and growth, such that infrequent fire and other disturbances that remove tree biomass may be sufficient to ensure maintenance of herbaceous vegetation. Hydrology and flooding disturbance may produce a variety of different grassland types, as may grazing by large herbivores (Noss, 2013). For the distinctive high-elevation grassland, southern Appalachian grassy balds, most researchers consider fire an unlikely explanation for these systems. Instead, the best-supported hypothesis is the "climate-herbivore hypothesis," which suggests that the balds were maintained by seasonal migratory megaherbivores, which grazed and browsed grassy tundra during Pleistocene glacial periods. After their extinction, these herbivores were replaced by native large herbivores (bison, *Bison bison*, and elk, *Cervus canadensis*) and later by livestock, which Euro-American settlers herded to the balds to graze in summer (Weigl & Knowles, 2014).

The area where eastern grasslands may have existed historically is not completely mapped because most eastern grasslands have been long lost to other land uses, primarily agriculture and, additionally, closed forests of dense trees that invaded after fire exclusion (Hanberry & Abrams, 2018). Expert-informed assignments of historical vegetation types are available in the LANDFIRE Biophysical Settings database (BPS; LANDFIRE, 2021), which supplies a starting point to indicate potential grassland locations throughout the eastern United States. Although extensive, this layer likely is an undercount of grasslands at 2.9 million ha because grassland locations mapped more intensively thus far total about 2.3 million ha in the mid-southeastern United States, primarily Kentucky and Tennessee (Figure 1; Southeastern Grasslands Initiative [SGI], 2021).

Given these discrepancies, it may be helpful for grassland conservation efforts to have a model of potential fire-maintained grassland locations throughout the eastern United States. Therefore, we applied fire proxies of wind speed, three measures of topography, and soil moisture to develop a simple ruleset of locations that may have been more probable to support fire-maintained grasslands under historical vegetation and fire conditions. This research extends previous work demonstrating that wind speeds delineated the Great Plains substantially better than moisture-related factors encompassing annual precipitation and its coefficient of variation, ratio of precipitation to potential evapotranspiration, climatic moisture index, and July vapor pressure (Hanberry, 2021). Given that these typically continuous climate-related variables were not able to distinguish an entire grasslands region, they are unlikely to make more subtle distinctions between intermixed grasslands and forests within an overall humid region, particularly as values for these variables did not vary with known grasslands. After modeling potential grasslands, we then documented when fire exclusion changed historical vegetation and fire conditions, resulting in transition to closed forests, in Kentucky, where eastern grasslands may have the greatest documentation (e.g., detailed grasslands mapped by SGI) aside from extensive documentation of pine savannas in the southeastern Coastal Plain (Platt, 1999).

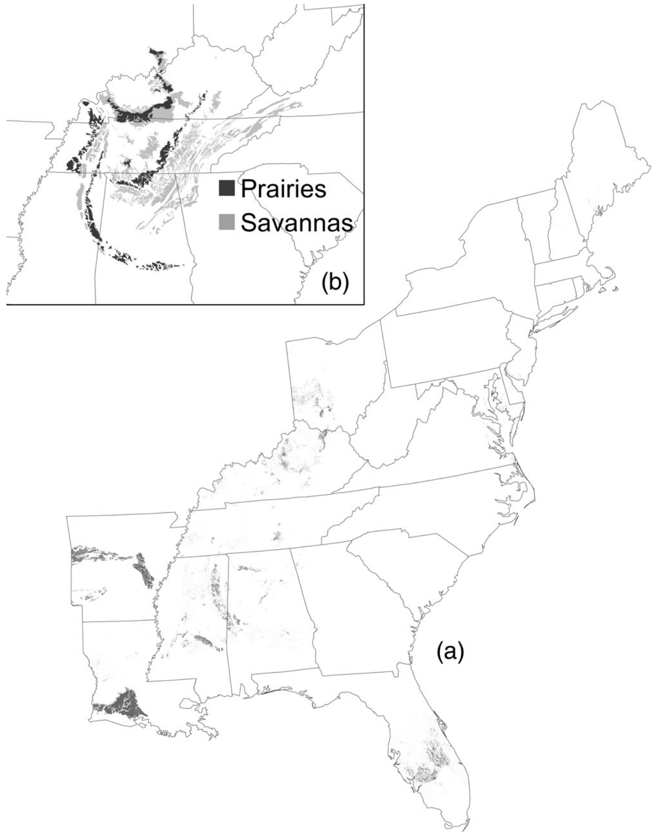

FIGURE 1 Locations of historical grasslands throughout the eastern United States according to LANDFIRE (a; 2021) and mapped historical grasslands in part of the southeastern United States (b; Southeastern Grasslands Initiative)

METHODS

The study extent was the eastern United States, where historical grassland locations are not fully compiled (Figure 1). That is, we excluded the Prairie Peninsula extension of the central North American grasslands or where grassland locations are relatively well known from historical reconstructions (Transeau, 1935). For modeling samples, we selected grasslands from LANDFIRE BPS (resolution of 30 m^2; LANDFIRE, 2021), which has expert-assigned vegetation types for the entire United States; however, assignments may not be accurate. To focus on differentiating likely locations for grasslands, we removed spruce, fir, and northern hardwoods. Then, we randomly sampled 100,000 points that were grasslands and 100,000 points that were ecosystem types of needle-leaved trees, broadleaf trees, or mixed forest, keeping in mind that some of these assigned non-grassland samples may have been grasslands. Indeed, 4500 non-grasslands points were grasslands (or savannas), according to SGI (2021; range of areas based on grassland shapes). Therefore, we switched those ecosystem type assignments and modeled with the combined BPS and SGI datasets. In addition, despite the limited extent, we modeled with the more detailed SGI dataset, with 40,000 samples of grasslands and 40,000 samples of non-grasslands. The current SGI dataset covers an area of about 8 million ha, including 5.8 million ha of savannas; the SGI dataset is a draft that will be iteratively refined. Because grasslands and savannas are on a continuum that is difficult and likely futile to separate, particularly in the eastern United States, we modeled with and without savannas.

For modeling, we partitioned the datasets into training (75% of samples) and test sets (withheld samples), trained the model with 10-fold cross-validation, and then predicted for the test sets with the caret package (Kuhn, 2008; R Core Team, 2021). For model variables, all of which had 250-m^2 resolution, we selected mean wind speed from the Global Wind Atlas, a downscaled version of the 30-km resolution of European Centre for Medium-Range Weather Forecasts ERA5 reanalysis of years 2008–2017 (these are wind models, not vegetation models but are informed by vegetation; Badger & Jørgensen, 2011; Global Wind Atlas, 2021; Hersbach et al., 2020); topographic difference measures of roughness, vector ruggedness, and terrain ruggedness (these topographic difference variables are calculated by different methods and smaller values equal flatter areas with less topographic difference; Amatulli et al., 2020); and soil water at 10 cm (Hengl & Gupta, 2019). We applied the random forests classifier to determine the most influential variables and reduced models to the most influential variable to develop a simple ruleset. Then, we employed the C5.0 classifier, which can supply an explicit ruleset. Random forests and C5.0 are both nonlinear classifiers, but they employ different decision processes; for example, random forests uses the Gini index for deciding the binary thresholds for subdividing data, whereas C5.0 applies entropy and information gain, which can result in multiple splits. Lastly, we predicted the ruleset to the eastern United States, removed water and most wetlands, and determined the 2016 land cover for these locations (resolution of 30 m^2; Homer et al., 2020).

RESULTS

Historical grassland locations throughout most of the eastern United States are unknown, which means that accuracy metrics only show a similarity of predictions to datasets. Compared with LANDFIRE, for predictions of withheld samples of the model with all variables, accuracy was 73%, with a true-positive rate (i.e., samples predicted as grasslands that were identified as grasslands by LANDFIRE) of 68% and a true-negative rate of 79%. The area under the curve (AUC) (i.e., the area under the receiver operating characteristic curve, which plots the true-positive rate compared with the false-positive rate at all classification thresholds) was 81%. Results from the combined LANDFIRE and SGI datasets were nearly the same, albeit after a relatively small change in sample assignments. The accuracy of the modeled complete grassland and savanna SGI dataset also was similar, at 75%. The accuracy of the modeled grassland-only SGI data was greatest, with an accuracy of 88% and AUC of 95%.

The two most influential variables were wind speed (value of 100 on a 100 scale of the contribution of each variable to model accuracy) and roughness (value of 78), followed by topographic roughness (value of 30), vector ruggedness (value of 26), and soil moisture (value of 0) for the LANDFIRE dataset. Results were nearly identical for the combined LANDFIRE and SGI datasets. For the complete SGI, the importance value of roughness was less influential (value of 51) and marginally less than the value for vector ruggedness (value of 56). For the grasslands-only SGI, the importance value of roughness was most influential (value of 100), with wind speed less important (value of 62), followed closely by the other topographic variables.

Singling out the most influential variables, for LANDFIRE, roughness alone had an accuracy of 69% correct predictions for both random forests and C5.0 classifiers, which was only a slight loss for a parsimonious model of one variable. Primarily, the accuracy loss was due to reduced true-negative rates to 70% (random forests classifier) and 72% (C5.0 classifier). The AUC values were 69% (C5.0 classifier) and 72% (random forests classifier). Wind speed was less accurate, with accuracies of 53% (random forests classifier) and 56% (C5.0 classifier). Roughness and wind speed combined only increased accuracy from 69% (both classifiers) to 70% (C5.0 classifier) or even decreased accuracy to 65% (random forests classifier). The combined LANDFIRE and SGI datasets duplicated these results; however, for modeling wind speed alone, the predicted true-positive rate increased and the true-negative rate decreased. For the complete SGI, results were similar, except that wind speed alone improved in accuracy, at 63% (random forests classifier) and 69% (C5.0 classifier). Modeling vector ruggedness alone produced the same accuracy as roughness. The grasslands-only SGI was most accurate. Accuracy was 85% (both classifiers) for roughness alone and 77% (both classifiers) for wind speed alone, which only slightly increased for the combined variables.

Regarding values of roughness, for LANDFIRE, the ruleset generated by the C5.0 classifier applied a threshold between grasslands and non-grasslands of 59; that is, grasslands occurred on flatter sites with less topographic difference. The combined LANDFIRE and SGI datasets increased the roughness threshold to 70 (Figure 2a). The complete SGI dataset increased the roughness threshold to 104, and the grasslands-only SGI dataset had a roughness threshold of 95 (Figure 2b). Despite relatively little difference in accuracy between predictions for models with one variable or more than one variable, predicted areas for roughness alone covered large extents, particularly demarcating the southeastern Coastal Plain. The increased roughness thresholds incorporated the slightly less flat areas of the exterior edges, in the southeastern Coastal Plain and up the Atlantic Coast and the Lower Mississippi Alluvial Valley, along with the plains of Ohio and New York.

As for values of wind speed, for LANDFIRE, the ruleset generated by the C5.0 classifier applied a threshold between non-grasslands and grasslands of 1.8 m s^{-1}. The combined LANDFIRE and SGI datasets increased the wind speed threshold to 2.8 m s^{-1} (Figure 2c). The

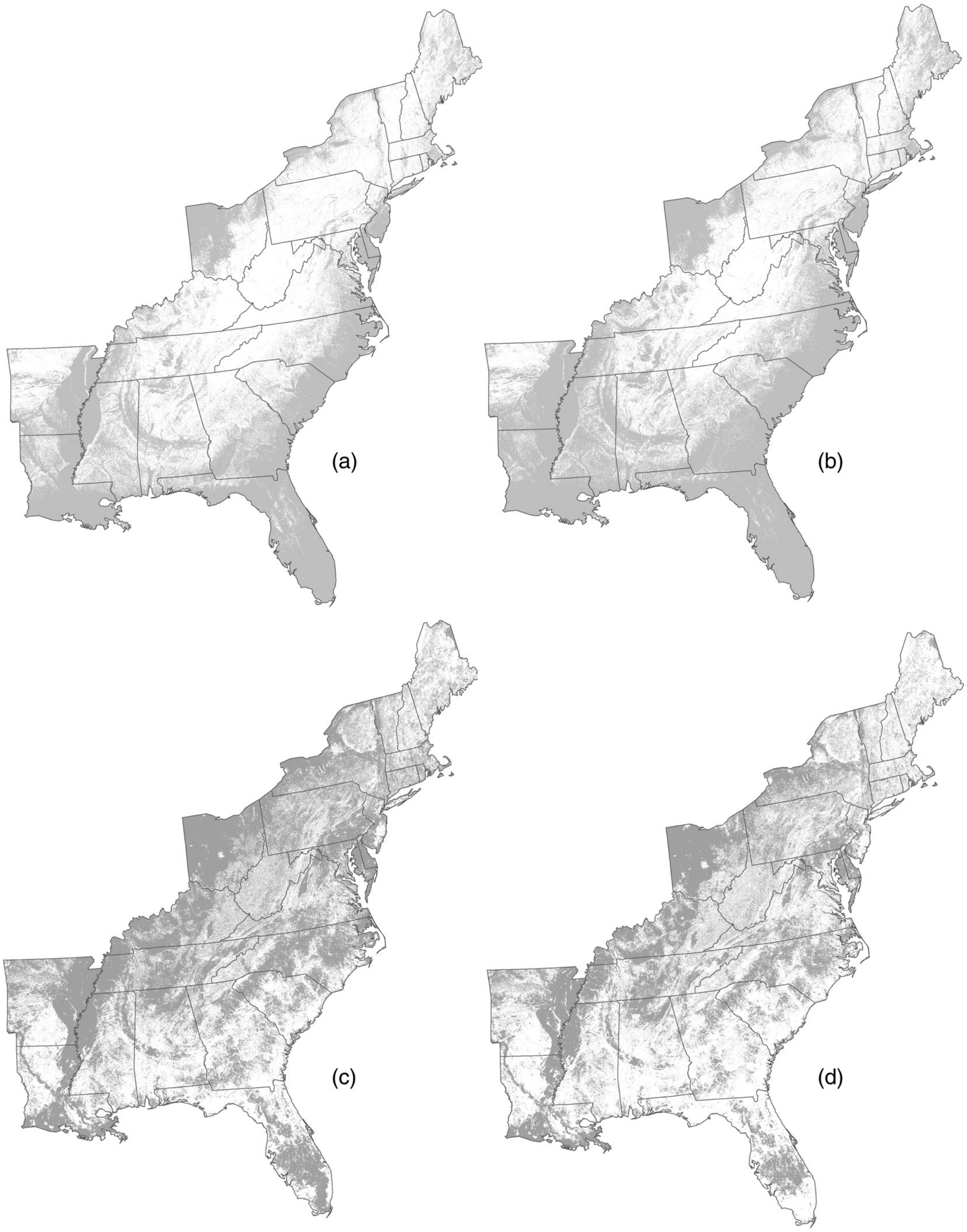

FIGURE 2 Area with roughness ≤70 (a), with roughness ≤95 (b), wind speed >2.8 m s^{-1} (c), and wind speed >3.4 m s^{-1} (d)

complete SGI dataset increased the wind speed threshold to 3.15 $m\ s^{-1}$, and the grasslands-only SGI dataset increased the wind speed threshold to 3.4 $m\ s^{-1}$ (Figure 2d).

We combined the roughness threshold of 95 and wind speed threshold of 3.4 $m\ s^{-1}$ from the most accurate grasslands-only SGI model, which balanced the area between the flat Coastal Plains and the interior uplands. Within these intersected thresholds, large wetlands, which may consist of not only wet prairies but also marshes, swamps, and riparian forests, specifically the Lower Mississippi Alluvial Valley, were included. Therefore, we removed ecological subsections that likely were predominantly swamps, marshes, or riparian forests (Cleland et al., 2007) and land cover of open water and woody wetlands (Homer et al., 2020).

Ultimately, the mapped potential grassland area was 27,101,145 ha (Figure 3). The predicted grassland locations overall appeared to match where grasslands should be (Figures 4 and 5). According to 2016 land cover, potential grasslands now are 40% crops, 25% pasture, 18% forests, 8% developed open space, 5% developed (i.e., building infrastructure), and about 1.5% each of herbaceous upland vegetation, shrubland, and herbaceous wetlands. We archived the potential grassland layer at the Forest Service Research Data Archive (https://www.fs.usda.gov/rds/archive/catalog/RDS-2021-0088).

DISCUSSION

Potential grasslands

To identify historical fire-maintained grasslands in the eastern United States, we can approximate frequent surface fire through wind and topography (i.e., the fire compartment concept), locating potential sites with conditions most likely to spread fire in the absence of

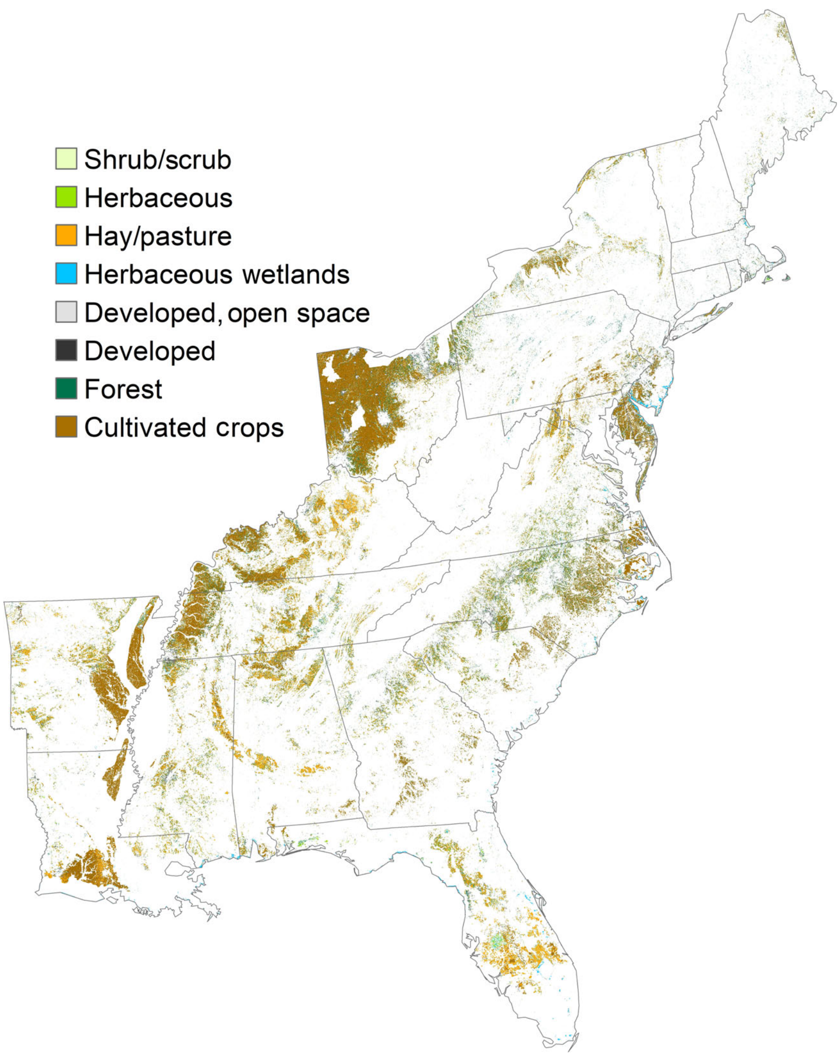

FIGURE 3 Locations of potential grasslands, with 2016 land cover classes (Homer et al., 2020)

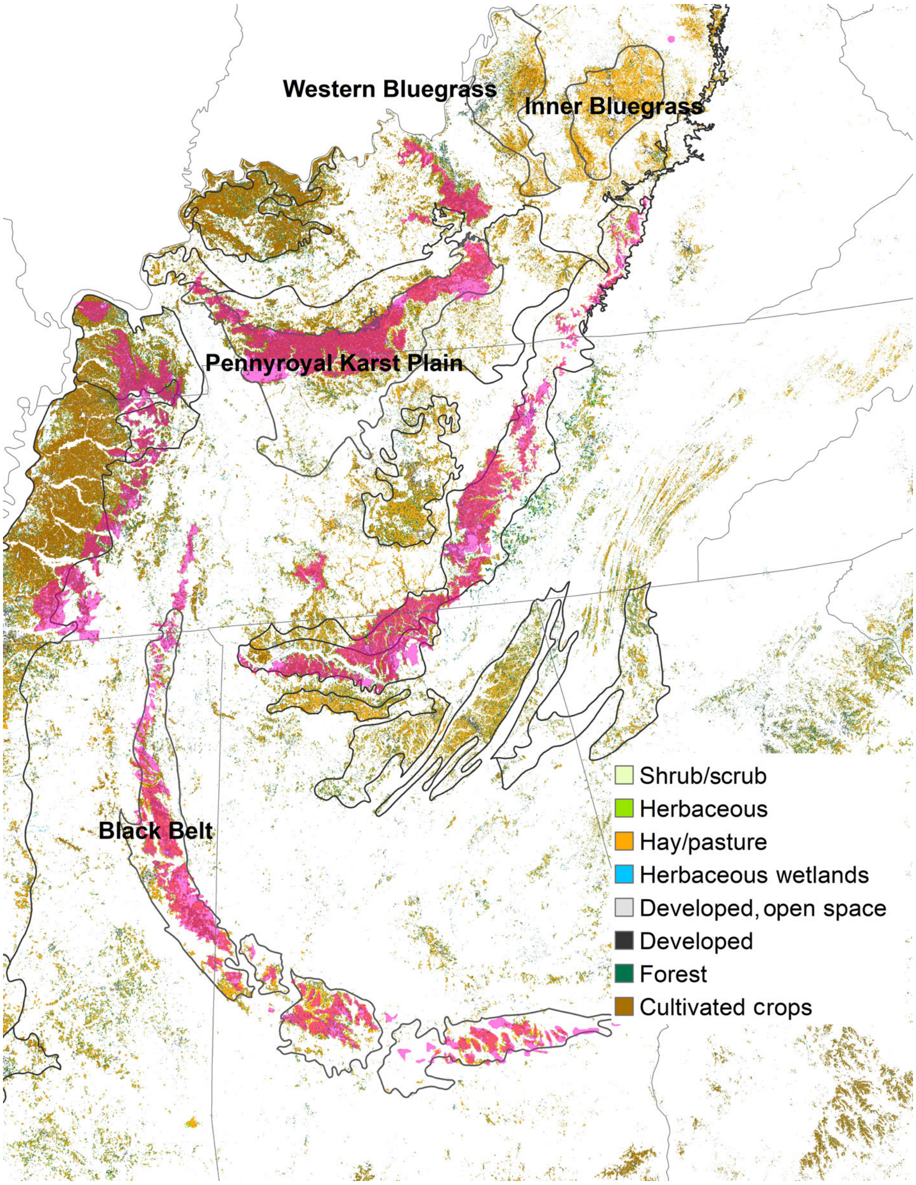

FIGURE 4 Locations of potential grasslands compared with grasslands mapped by the Southeastern Grasslands Initiative (2021; pink), with outlined ecological subsections likely to be ≥20% grasslands

information about historical fuels, ignitions, or grassland distributions. Relatively undegraded grasslands currently cover a poorly documented yet small percentage of land area in the eastern United States, due to typically a >95% loss, and most fuel conditions have been altered through conversions to closed forests or land uses, including roads that disrupt fire spread (Noss et al., 1995). Because surface fire is important for reducing tree densities, this modeling generated potential grassland locations throughout the eastern United States, resulting in coverage that was more extensive than the SGI dataset (SGI, 2021) and more detailed than the LANDFIRE BPS (LANDFIRE, 2021). Potential treeless grasslands covered 27 million ha, or 14% of the 200 million ha of the eastern United States, compared with 2.9 million ha from LANDFIRE and 2.2 million ha plus 5.8 million ha of savannas from SGI.

A generalized ruleset was that grasslands occurred at topographic roughness values less than 95, or flatter locations, and wind speeds ≥3.4 m s^{-1}, based on the grasslands-only SGI dataset. As indicated by the modeling process, soil moisture was not influential, because fires can occur over a range of soil moistures in the eastern United States. The ruleset modeled on the full SGI dataset, including savannas or the portion of the continuum between grasslands and open forests, resulted in both an increase in roughness and a decrease in wind speed, which is consistent with reduced probability of fire. Mean wind speed patterns, at least at coarsely modeled

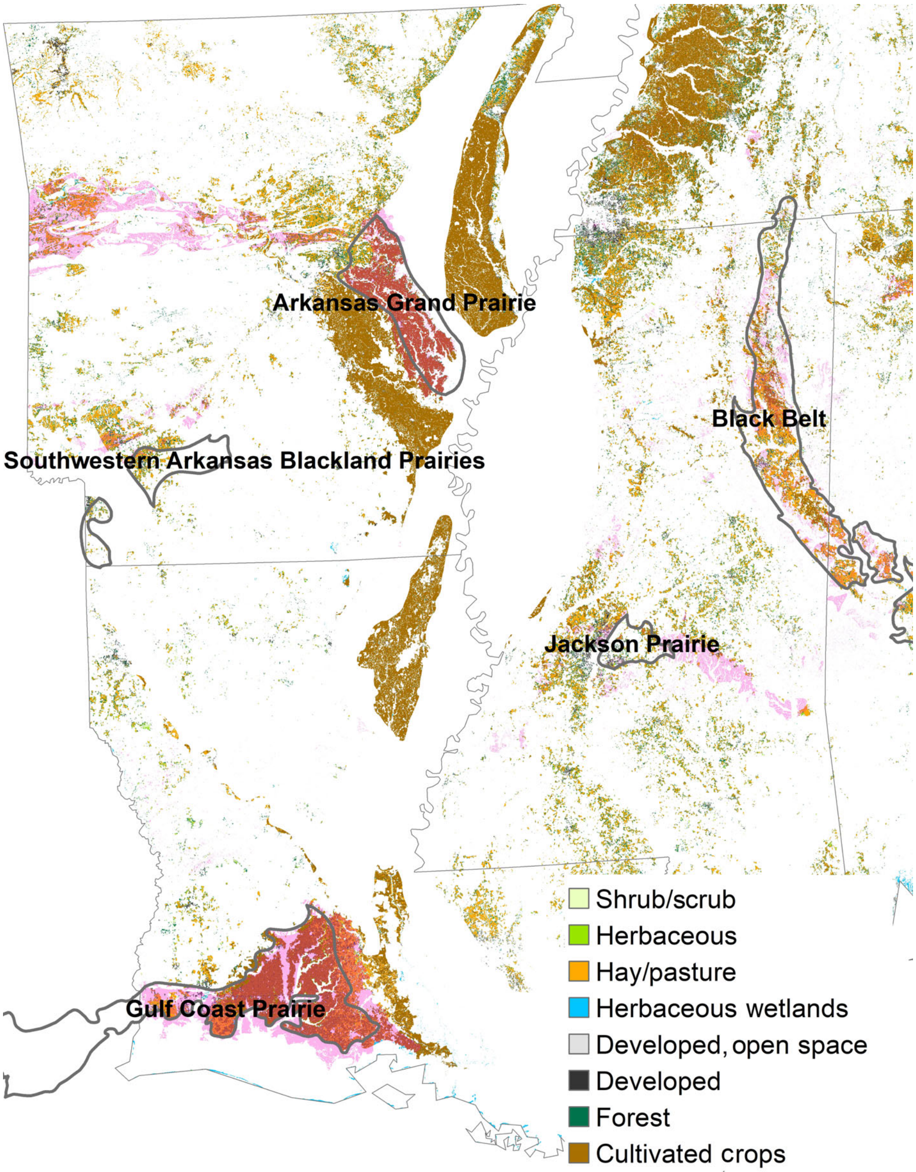

FIGURE 5 Locations of potential grasslands compared to grasslands mapped by LANDFIRE (2021; pink), with outlined and named ecological subsections identified as grasslands

scales for general thresholds of potential grasslands, overall have remained relatively stable during at least the past 10,000 years (Hanberry, 2021). Therefore, we expect that modeled wind speeds during 2008–2017 are representative of historical long-term patterns. For future wind speeds, projected mean wind energy densities are highly variable in location and sign of change, but changes in magnitude are likely to be less than 15% (Pryor & Barthelmie, 2011). However, wind speeds have become nearly irrelevant because large fire compartments associated with wind spread are not operational due to land cover and use changes over most of the eastern United States. Wildfires may increase in the future, perhaps with increased probability in potential grassland locations. Generally, most future fires will be planned and fall within prescribed limits, likely during low wind speeds to increase control over the prescribed burn.

Potential grasslands included the major known grasslands of the Big Barrens (Pennyroyal Karst Plain) prairies in Kentucky and Tennessee, the Black Belt Prairie, Jackson Prairie, Arkansas Grand Prairie, Gulf Coastal Prairie, and Florida Dry Prairie, a hyperseasonal subtropical grassland of south-central Florida (Orzell & Bridges, 2006). Predictions generally were similar to the LANDFIRE and SGI datasets and grassland ecological subsections (Figures 4 and 5). Some disagreement in locations was evident among sources, for example, the Jackson Prairie and Arkansas Grand Prairie, where location placements ranged along a west-to-east trajectory (Figure 5). It may be that fire initiates in the favorable location and then spreads eastward with the prevailing winds beyond those bounds. Figures from other mapped sources appear to match as well, including scattered grasslands over most of Pennsylvania (Pennsylvania Game Commission, 2021), albeit compiled and digitized locations of eastern grasslands are not readily available. As mapped grassland layers become available, these will help validate the potential grassland layer.

Generally, relative proportions of grasslands throughout the eastern United States seem reasonable, as historically, open forests increased from north to south, and grassland proportions reflected the same gradients. Even without temperature variables, less than 2% of the northernmost parts of the northern states, that is, the northern mixed forests, were predicted to be grasslands. Specifically, the areas identified in northern Maine may be unlikely to have grasslands in a colder climate with a limited fire window. The central eastern region, or historically open oak forests, was 10% grasslands. The southeastern region, or historically open pine or pine-oak forests, was 15% grasslands. Although the Coastal Plain had conditions appropriate for treeless grasslands, the region historically was dominated by longleaf pine (*P. palustris*), which is highly adapted to surface fire incorporating even a "grass" stage, with the presence of other pine species (e.g., *Pinus echinata*, *Pinus elliottii*, *Pinus densa*, *Pinus serotina*, and *Pinus taeda*).

The predicted grassland areas are potentially overestimated relative to the amount of realized historical grasslands. That is, we predicted conditions that were suitable for grasslands and may be more likely to support grasslands but, with decreasing probability along a tree density continuum, may have been savannas, open and closed woodlands, or closed forests. Specifically, the predicted grassland areas may have overlapped with potential savannas. Just as SGI includes savannas in its grasslands definition, it may be nonsensical, particularly in the historical eastern open forest matrix, to separate whether a location should be grassland or savanna. Indeed, locations may lose and gain tree density as fire ignition frequency or other conditions change over time.

Identification of wet grasslands also is important, but because some wet grasslands may be less influenced by fire, models based on fire proxies of topography and wind speed may not be tailored specifically to wet grassland identification. Nonetheless, in Florida, wet prairie is estimated to have a fire-return interval of 2–3 years and glades marshes in the Everglades have an estimated fire-return interval of 3–10 years, burning even when inundated, similar to coastal marshes (Florida Natural Areas Inventory, 2010). Indeed, herbaceous wetlands characterized most of the recent large fires in the eastern United States (Hanberry, 2020a). Even though we excluded ecological subsections that predominantly were swamps, marshes, or riparian forests, some wet extents remained, specifically in western Ohio, Florida, and along the Ohio and Mississippi Rivers in Kentucky and Tennessee. Western Ohio historically included a complex mosaic of swamps, including the Great Black Swamp, marshes, wet prairies, and prairies, which have been drained and converted to agriculture, along with oak open forests and beech (*Fagus grandifolia*)-dominated closed forests. A parallel situation occurred in Florida, in the wetlands and upland prairies surrounding the Everglades that have been converted to sugarcane, citrus groves, and cattle ranches; the latter, however, contain seminatural grasslands with grassland species of conservation concern (Noss, 2013). Probably riparian forests overall occurred along the Ohio and Mississippi Rivers, but in some locations, conditions may have been appropriate for grasslands, as demonstrated in the Lower Mississippi River Alluvial Valley (Figure 5).

Because relatively little is known about historical grassland locations, or sources of information are inaccessible, a comprehensive map of potential eastern grasslands is a progressive step for the recovery of grasslands and biodiversity conservation. Although treeless grassland locations may overlap with treed savannas or woodlands, restoration of either ecosystem state is valuable to support declining plant and animal species, many of which are endemic and imperiled (Hanberry & Thompson, 2019; Noss, 2013). Vertebrates include grassland subspecies, which range from the northeastern to southeastern United States, such as the extinct heath hen (*Tympanuchus cupido cupido*, i.e., the greater prairie chicken) and the endangered Florida grasshopper sparrow (*Ammodramus savannarum floridanus*). Forbs present in grassland and open forests in particular may be necessary for pollinators, which are declining. Biodiversity also includes fire-dependent fungi (Semenova-Nelsen et al., 2019).

Regarding restoration in the face of climate change, grassland restoration will provide increased resilience to ecosystems. Indeed, changing conditions make action more urgent to reduce risk. Wildlife species that are declining due to non-climate stressors have lower adaptive capacity, but grassland ecosystems provide critical resources for survival, growth, and reproduction that will help support wildlife in a changing climate. In addition to progressive warming and more extreme fire weather days, near-present and future changes typically encompass increased variability and range, with higher high and lower low values for many variables, including drought (Hanberry, 2020b). Grassland species overall are very tolerant of fire, wind, drought, and heat, particularly compared with mesic tree species of current broadleaf forests, which will protect grassland ecosystems against flash droughts, fires, and warming temperatures that may generate disastrous die-offs in current broadleaf forests. Grasslands by definition do not spread long flame lengths of severe fires, which threaten human infrastructure, and grassland species will never die from overstory tree boring and defoliating insects and disease. Grasslands have low water consumption, unlike dense broadleaf forests, allowing greater water resources for human use. Massive tree die-offs and increased fire and overstory tree insect and disease activity appear to be pathways that will benefit grassland ecosystems, making restoration easier and more desirable. Historical ecosystems are not outdated or doomed under future climate change because historical ecosystems are more tolerant of heat, drought, fire, flooding, and insects than current closed forest ecosystems, which may collapse under climate stress.

Historical accounts of state shifts from grasslands to forests

Surface fire has been excluded from areas where it was historically frequent. Fire exclusion involves cultural shifts from deliberate ignitions for prescribed burns to actively suppressing fires, creating fire breaks that disrupt vegetation continuity through land uses such as roads and harvested fields, and facilitating transitions to closed forests that are not able to spread surface fire due to protected conditions and lack of fine herbaceous fuels. The abundance of herbaceous vegetation, especially highly flammable grasses (Fill et al., 2016), reinforces surface fire regimes, whereas tree growth that reduces fine fuels from herbaceous vegetation will suppress surface fire regimes, with the exception of highly flammable pine needles and pyrophytic oak leaves (Ellair & Platt, 2013; Kane et al., 2008). Surface fires require enough moisture to grow herbaceous fuels followed by drying of the green vegetation to allow ignition as opposed to crown fires, which occur when drought and extreme fire weather permit coarse fuels from trees to burn. It may be that deliberate ignitions are superfluous in the southeastern Coastal Plain, where lightning strike density is the greatest of any large region in North America (Noss, 2018), but as little as 10% anthropogenic land cover may disrupt the flow of surface fires (Duncan & Schmalzer, 2004). Fire breaks as narrow as wagon tracks and furrows, as well as back burns, were historical safety strategies to stop fire spread.

Although not all grassland types may support closed forests, one frequent observation in historical accounts is dense growth of young trees trailing Euro-American settlement. Initially, settlers widely continued the practice of burning, often for livestock forage. For example, Sargent (1884, p. 545) mentioned that livestock may start grazing 4–6 weeks earlier due to February burns. Eventually crop cultivation, in combination with other land use changes and cessation of prescribed burns, resulted in the shift to fire exclusion.

Observations in Kentucky were numerous, as this western area was settled later than most eastern grasslands. Sargent (1884, p. 545) documented: "In Barren, Edmonson, and other counties extensive tracts of prairie existed at the time of the earliest settlement of the state. The presence of these prairies in the midst of a heavily-timbered region is ascribed to the annual burning to which they were subjected by the [native humans]. With the disappearance of the [native humans] trees sprang up, and this region is now well covered with a vigorous growth of black oaks of different species." For another example, Owen (1856, p. 83) recorded: "The old inhabitants of that part of Kentucky all declare that when the country was first settled it was, for the most part, an open prairie district, with hardly a stick of timber sufficient to make a rail, as far as the eye could reach, where now forests exist of trees of medium growth, obstructing entirely the view. They generally attribute this change to the wild fires which formerly use to sweep over the whole country, in dry seasons, being now, for the most part, avoided or subdued, if by accident they should break out. Since the settlement of the country this grass has almost become extinct, whereby opportunity has been afforded for timber to take root and flourish."

It is possible to extract from historical accounts a general range of dates for locations when cultural and ecosystem transition occurred. Shaler (1888, p. 27) described Kentucky as primarily continuous forests that were "singularly open, so that the early track-ways and wagon roads were easily made through them." When annual burning ceased around the year 1790, dense growth of young forests developed within 20 years, which was more difficult to clear than the primeval forests (Shaler, 1888, pp. 29–30). Davidson (1840, p. 32) declared: "The destitution of timber in the Barrens was owing to the frequent burning of the prairie by hunters to drive out the game, by which means the young and tender shoots were scorched and destroyed … With the advancing settlement of the country, the prairie fires were gradually extinguished, and the young timber had liberty to grow. The consequence is, that tracts which were destitute of shade ten to twenty years ago, are now covered with extensive forests of Black Jack, or scrub oak …" Based on these accounts, grasslands transitioned to forests within a 20-year interval; tree species that first established were the species already present, predominantly oaks, according to accounts. Transition initiated during approximately the years 1790–1810 and was evident by 1810–1830, depending on the location of settlement. That is, grasslands that were settled earlier also transitioned earlier than grasslands settled at later dates. Moreover, population or lightning strike density may not matter as much as landscape conversion through fire breaks of agriculture and roads (Gleason, 1922).

CONCLUSIONS

Finding the forgotten grasslands of the eastern United States is an essential first step for rediscovering and managing eastern grasslands, which are vital sources of biodiversity associated with open conditions, specifically plentiful grasses, forbs, insects, and grassland birds, which are the most highly imperiled habitat category of birds (Rosenberg et al., 2019). According to our models, potential fire-maintained grassland area covered 27 million ha compared with 2.9 million ha from LANDFIRE and 2.2 million ha of grasslands and 5.8 million ha of savannas from SGI, estimates that likely will increase after revision. A generalized ruleset was that grasslands occurred in relatively flat landscapes with roughness values less than 95 and wind speeds $\geq$3.4 m s^{-1}. However, predicted grassland locations also are likely to contain savannas and a range of tree densities. Indeed, after fire exclusion, and particularly land conversion that prevents low-severity fire spread, grasslands transitioned to young tree growth within 20 years, at least in Kentucky. In the eastern United States, potential grasslands now are 40% crops, 25% pasture, 18% forests, 13% developed open space and building infrastructure, and about 1.5% each of herbaceous vegetation, shrubland, and herbaceous wetlands. These remnants are not well positioned to maintain grassland biodiversity without extensive restoration and management.

AUTHOR CONTRIBUTIONS

Brice B. Hanberry conceived the ideas, designed the methodology, collected and analyzed the data, and led the writing of the manuscript. Reed F. Noss revised it critically, adding important intellectual content. Both authors contributed substantially to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Forest Service Research Data Archive: https://www.fs.usda.gov/rds/archive/catalog/RDS-2021-0088.

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