Forest Ecology and Management 477 (2020) 118468

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Predictors of fire-tolerant oak and fire-sensitive hardwood distribution in a fire-maintained longleaf pine ecosystem

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ARTICLE INFO

Keywords:
Longleaf pine
Pinus palustris
Oaks
Quercus spp
Fire-adapted hardwoods
Mast-dependent wildlife
Prescribed fire
Ecological restoration

ABSTRACT

The longleaf pine (*Pinus palustris*) ecosystem has been reduced to a fraction of its original extent, and where this ecosystem does occur, it is often degraded by hardwood encroachment. The reduction of hardwood tree cover is often a desirable longleaf pine community restoration outcome, though hardwood midstory and overstory trees have been recognized as an important natural component of the communities. Moreover, the appropriate amount of hardwood tree cover in a restored longleaf pine community is debated, as more hardwood tree cover can benefit mixed forest and mast-dependent wildlife (e.g., fox squirrels [*Sciurus niger*], white-tailed deer [*Odocoileus virginianus*]), and less hardwood tree cover is critical to the federally endangered red-cockaded woodpecker (*Leuconotopicus borealis*). To inform the debate, we assessed the environmental (e.g., topography, edaphic conditions, and pine basal area) and management (e.g., distance to firebreaks, prescribed fire history) factors that influenced abundance of upland hardwood trees in xeric longleaf pine communities on a site where frequent growing-season fire has been ongoing since 1991. We counted upland hardwoods ≥5 cm diameter at breast height (DBH) at 307 random field plots (0.04 ha) and categorized all hardwood trees as belonging to either a guild of fire-tolerant oaks or a guild of fire-sensitive hardwood species. We used generalized linear models (GLM) to determine the most important predictors of abundance for both guilds. The predictors of abundance differed between the two guilds, with fire-tolerant oak abundance increasing with greater slope and proximity to ignition sources and decreasing with greater pine basal area. Fire-sensitive hardwood abundance increased with mesic site conditions and decreased with the number of growing-season fires and greater pine basal area. Although seasonality in fire history was an important predictor of fire-sensitive hardwood abundance, variables related to long-term fire-history were not important predictors of fire-tolerant oak abundance in longleaf pine communities. However, with limited variation in fire return interval across the study area, our ability to draw inferences regarding the role of fire return interval was limited. Where hardwood encroachment is not a problem, and hardwood levels are below desired, balanced target levels, hardwood abundance in longleaf pine communities can be increased by reducing pine basal area and reducing prescribed fire intensity.

1. Introduction

The floral and faunal communities of the fire-dependent longleaf pine ecosystem are integral contributors to the biodiversity hotspot associated with the southeastern United States (Noss et al., 1995). In the absence of frequent fire, upland longleaf pine communities can become susceptible to hardwood encroachment, which can have deleterious effects on longleaf pine regeneration and herbaceous plant composition. Prescribed fire often is used during restoration aimed at creating a longleaf pine dominated overstory with an understory of grasses and forbs (USFWS, 2003; Brockway et al., 2005). Moreover, reducing the stature and abundance of midstory and overstory hardwood trees in longleaf pine uplands is a common motive driving prescribed fire management (Gilliam and Platt, 1999; Hiers et al., 2014). Although hardwood tree reduction is often an integral component of longleaf pine restoration, long-term management requires a complex understanding regarding the ecological role of upland hardwoods in the ecosystem.

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https://doi.org/10.1016/j.foreco.2020.118468
Received 18 May 2020; Received in revised form 20 July 2020; Accepted 26 July 2020
Available online 14 August 2020
0378-1127/

Management in longleaf pine communities typically aims to achieve reduction or removal of upland hardwood cover with the goal of providing habitat for the federally endangered red-cockaded woodpecker (Garabedian et al., 2017). Although removal or substantial reduction of hardwood canopy and midstory cover benefits those species dependent on the resulting conditions, recent research has called attention to the ecological value of retaining upland hardwoods (Perkins et al., 2008; Hiers et al., 2014; Lashley et al., 2014). Hence, the appropriate amount of upland hardwood cover in restored longleaf pine communities is debated, as more hardwood cover can provide heterogeneity in forest composition and structure (Hiers et al., 2014), escape cover or wildlife refugia (Conner et al., 2009), and mast as food for wildlife (Perkins et al., 2008; Lashley et al., 2014). Conversely, maintaining low levels of hardwood cover is important to for providing habitat for the federally endangered red-cockaded woodpecker (Garabedian et al., 2014, 2017). Although, the presence of upland hardwoods in longleaf pine communities has been recognized as ecologically valuable (Landres et al., 1990; Greenberg and Simons, 1999; Hiers et al., 2014; Loudermilk et al., 2016), management efforts often strive to achieve narrow targets which typically include the goals of reducing persistent hardwood cover and preventing hardwood establishment in upland areas.

Within the longleaf pine ecosystem, hardwood tree species have complex relationships with fire, edaphic conditions, topography, and local canopy composition and structure (Gilliam et al., 1993; Jacqmain et al., 1999; Addington et al., 2015b; Whelan et al., 2018). For example, research indicates that some oak species present in longleaf pine uplands are fire-tolerant (Rebertus et al., 1989; Greenberg and Simons, 1999; Cavender-Bares et al., 2004; Hiers et al., 2014). Thick bark, ability to re-sprout after fire, and reproduction at small sizes have been implicated as evolutionary adaptations to frequent fire (Jackson et al., 1999; Greenberg and Simons, 1999; Cavender-Bares et al., 2004; Hiers et al., 2014), and when these adaptation are coupled with local variation in fire regime, some hardwoods are able to escape fire mortality in frequently burned upland longleaf pine communities (Hoffmann et al., 2020). Conversely, sensitivity to frequent fire has been reported for a different subset of hardwoods present in upland longleaf pine communities (Boyer, 1990; Haywood et al., 2001; Addington et al., 2015b). In addition to fire frequency, the effect of fire seasonality has been the focus of numerous investigations into hardwood tree dynamics (Glitzenstein et al., 1995; Brockway and Lewis, 1997; Haywood et al., 2001; Glitzenstein et al., 2012; Addington et al., 2015a, b; Whelan et al., 2018). Although the reported influence of fire season varies in the literature, fire conducted during the dormant season is less likely to cause mortality or top-kill of hardwoods than growing-season fires, and repeated dormant-season burning results in greater hardwood abundance than with repeated growing-season burning (Boyer, 1990; Streng et al., 1993; Glitzenstein et al., 1995).

Edaphic conditions and topographic characteristics influence forest composition and structure, including hardwood tree abundance, directly through species-site associations and indirectly by influencing fire behavior (Gilliam et al., 1993; Jacqmain et al., 1999; Addington et al., 2015b). Slope, aspect, elevation, and topographic position are intrinsically linked to soil properties such as texture, moisture, and associated nutrient availability (Jenny, 1994). The effects of topography and soil conditions act either individually, or in combination, to influence forest microclimate, and determine hardwood tree species composition and abundance. Importantly, complex vegetation-fire feedback mechanisms operate throughout longleaf pine ecosystems, wherein environmental conditions influence fire behavior and the composition and density of trees (Fill et al., 2015). Environmental conditions and the resulting plant communities influence fire spread and intensity by affecting the type, continuity, and moisture of fuels (Kane et al., 2008; Wenk et al., 2011; Crandall and Platt, 2012; Wiggers et al., 2013; Addington et al., 2015b; Fill et al., 2015). Topography can influence fire behavior by increasing fire intensity associated with upslope head fires and decreasing intensity associated with downslope backing fires (Rothermel, 1983; Addington et al., 2015a).

Hardwood tree abundance in upland longleaf pine communities can vary depending on site conditions and fire management, and thus the abundance of hardwood trees is an appropriate indicator of how hardwood communities respond to both long-term fire management and ecological gradients. For example, an assemblage of oaks (e.g., *Quercus incana* [bluejack oak], *Q. laevis* [turkey oak], *Q. margarettae* [sand post oak], *Q. marilandica* [blackjack oak], *Q.* stellata [post oak]) in longleaf pine sandhills are more abundant in xeric conditions and on upper slopes and ridges with sandy well-drained soils (Gilliam et al., 1993; Peet and Allard, 1993; Jacqmain et al., 1999; Cavender-Bares et al., 2004; Sorrie et al., 2006; Hiers et al., 2014). Conversely, other hardwood trees (e.g., *Acer rubrum* [red maple], *Liquidambar styraciflua* [sweetgum], *Nyssa sylvatica* [blackgum], *Prunus serotina* [black cherry]) favor mesic conditions and are more prevalent on lower slope areas with fine-textured soils (Gilliam et al., 1993; Jacqmain et al., 1999; Carr et al., 2010; Addington et al., 2015b). Further, other hardwood species (e.g., *Carya* sp. [hickory], *Cornus florida* [flowering dogwood], *Diospyros virginiana* [common persimmon], *Quercus falcata* [southern red oak], *Q. nigra* [water oak], *Q. velutina* [black oak]) may have less specific associations with edaphic conditions or topography, and their presence or abundance is affected by the interaction among fire, edaphic conditions, and topography (Gilliam et al., 1993; Jacqmain et al., 1999).

In addition to edaphic conditions and topography, hardwood tree distributions are related to both overstory pine basal area and proximity to fire ignition sources (Lashley et al., 2014; Addington et al., 2015a, b). As overstory pine basal area decreases, the likelihood of hardwood release into the midstory and overstory increases, which may be attributed to less competition for light, space, water, or nutrients (Knapp et al., 2014; Addington et al., 2015b). Moreover, areas with sparse overstory pine result in less litter of flammable pine needles, and can have decreased fuel continuity when compared to areas with dense overstory pine which in turn can cause patchy burns and reduced hardwood mortality (Jacqmain et al., 1999; Addington et al., 2015a, b; Whelan et al., 2018). Also, distance from firebreaks is an important predictor of hardwood tree abundance, with increased densities of hardwood trees in close proximity to firebreaks because fire intensity is presumably lower near the source of ignition (Jacqmain et al., 1999; Lashley et al., 2014).

Previous research has explored predictors of understory and midstory hardwood distribution in longleaf pine communities (Streng et al., 1993; Provencher et al., 2001; Knapp et al., 2014; Addington et al., 2015a, b; Whelan et al., 2018), but the predictors of hardwood tree abundance in the fire-maintained longleaf pine ecosystem has been less studied (but see Glitzenstein et al., 1995; Jacqmain et al., 1999; Addington et al., 2015b). Studies that have investigated hardwoods in the longleaf pine ecosystem have either lacked long-term fire history data (Jacqmain et al., 1999), or combined all hardwood species as a single response variable rather than model the distribution of individual species or guilds (Boyer, 1990; Boyer, 1993; Streng et al., 1993; Glitzenstein et al., 1995). We address this gap by modeling the distributions of two guilds of hardwood trees on a landscape that has been managed with long-term frequent fire.

Our objective was to examine the role of long-term frequent fire and environmental conditions in predicting abundance of two guilds of hardwood species present in upland longleaf pine communities: fire-tolerant oaks (FTO) and fire-sensitive hardwoods (FSH). Hence, our goal was to identify predictors of FTO and FSH abundance resulting from 28 years of frequent prescribed fire. We expected abundance of FTO to be predicted best by xeric conditions such as steep slopes, ridges, and sandy soils regardless of fire history. We expected abundance of FSH to be predicted best by fire history and mesic site conditions such as those present on lower elevation sites and sandy loam soils. Our goal was not to challenge the importance of frequent fire and hardwood stem reduction for restoring longleaf pine communities, but to identify

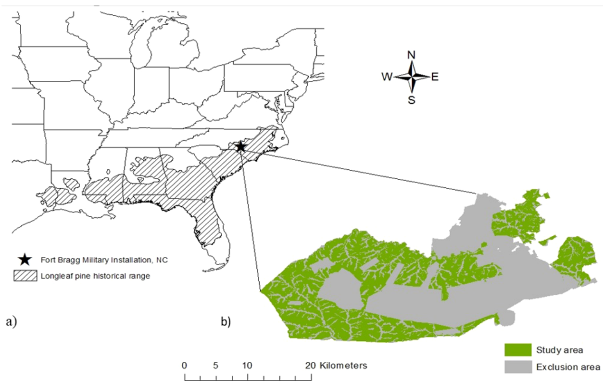

Fig. 1. Study area in relation to the historical range of the longleaf pine ecosystem (a), and the upland study area and exclusion areas (b). Fort Bragg Military Installation, North Carolina, USA, 2018.

aspects of long-term fire management and site conditions that influence FTO and FSH persistence following decades of prescribed burning.

2. Materials and methods

2.1. Study area

We conducted the study on Fort Bragg Military Installation, located in the Sandhills physiographic region of south-central North Carolina, USA (35.1°N, −79.2°W; Fig. 1). Fort Bragg is a 625-km^2 military base that is among the most important remnant areas of the longleaf pine-wiregrass (*Aristida stricta*) ecosystem in the southeastern United States. Management of longleaf pine-wiregrass communities on Fort Bragg is focused on conserving endangered species (e.g., the federally endangered red-cockaded woodpecker [*Leuconotopicus borealis*]), and maintenance of troop training facilities and infrastructure (FBMI, 2018). To achieve management goals, Fort Bragg implements a 3-year rotation of early, growing-season fire wherein approximately one-third of the base is burned each year (Cantrell et al., 1995; Lashley et al., 2014; FBMI, 2018). Frequent growing-season fire has been used as the dominant management strategy since 1990; however, land managers also incorporate dormant-season prescribed fire to meet burn quotas not achieved with growing-season burning (Lashley et al., 2014; FBMI, 2018).

The landscape is characterized by rolling hills dissected by streams, bottomlands, and stream-head pocosins (Sorrie et al., 2006; FBMI, 2018). The elevation ranges from 36 m to 183 m above sea level. The uplands (> 90% of the landscape) typically are composed of deep, well-drained sandy soils with the most common soil series being Candor sand and Lakeland sand (Sorrie et al., 2006; Soil Survey Staff, NRCS, 2018; FBMI, 2018). The lower slopes are comprised of loamy sands (e.g., Blaney loamy sand, Gilead loamy sand), and loam soils (e.g., Johnston loam) comprise the bottomland areas (Cantrell et al., 1995; Sorrie et al., 2006; Soil Survey Staff, NRCS, 2018; FBMI, 2018). The climate is characterized as sub-tropical with long, hot summers and short mild winters. The average maximum daily temperature and the average monthly precipitation peak in July at 33 °C and 150 mm, respectively, whereas the average maximum daily temperature is lowest during January (12 °C; [FBMI, 2018]). The average annual precipitation is approximately 1129 mm/year, and the average annual temperature is 16 °C (FBMI, 2018). The majority of Fort Bragg is comprised of pine/scrub oak sandhill community in which longleaf pine, wiregrass, and oaks (*Quercus* spp.) are the dominant plant species (Cantrell et al., 1995; Sorrie et al., 2006). Other vegetative communities include upland hardwood, bottomland hardwood, and managed grasslands (Sorrie et al., 2006; Lashley et al., 2014). Common hardwood tree species include turkey oak, blackjack oak, sweetgum, sand post oak, and blackgum (Lashley et al., 2014; Sorrie et al., 2006).

Table 1
Species categorized as fire-tolerant oaks and fire-sensitive hardwoods, number of plots where present, occurrence (% of plots), and total number of stems counted at 307 inventory plots (0.04 ha). Fort Bragg Military Installation, North Carolina, USA, 2018.

Species	Plots	Occurrence (%)	Total
Fire-tolerant oaks			
Bluejack oak (*Quecrus incana* Bartr.)	20	2.66	50
Blackjack oak (*Quercus marilandica* Muenchh)	72	24.60	463
Post oak (*Quercus stellata* Wang.)	17	2.34	44
Sand post oak (*Quercus margaretta* Ashe.)	46	10.26	193
Southern red oak (*Quercus falcata* Michx.)	28	3.72	70
Turkey oak (*Quercus laevis* Walt.)	105	39.64	746
Total	–	–	1566
Fire-sensitive hardwoods			
Black cherry (*Prunus serotina* Ehrh.)	1	0.05	1
Blackgum (*Nyssa sylvatica* Marsh.)	10	0.96	18
Black oak (*Quercus velutina* Lam.)	13	2.66	50
Butternut (*Juglan cinerea* L.)	2	0.16	3
Flowering dogwood (*Cornus florida* L.)	15	2.76	52
Hickory (*Carya sp.*)	27	3.88	73
Persimmon (*Diospyros virginiana* L.)	6	0.32	6
Red maple (*Acer rubrum* L.)	1	0.05	1
Sweetgum (*Liquidambar styraciflua* L.)	13	3.45	65
Water oak (*Quercus nigra* L.)	8	2.50	47
Total	–	–	316

2.2. Site selection and data collection

To strengthen our ability to make inferences about upland hardwood tree abundance, we eliminated all areas within 50 m of streams, classified wetlands, bottomland hardwood communities, and areas managed for early successional plant communities. We counted and identified all trees ≥5-cm diameter at breast height (DBH) at 307 randomly located 0.04-ha circular inventory plots (~11.4-m radius, ~408.3 m^2) in upland longleaf pine communities. We used 5-cm DBH as a cut-off to define tree-sized hardwoods based on previous research on the minimum size at maturity of common hardwoods in upland longleaf pine communities (Greenberg and Simons, 1999; Cavender-Bares et al., 2004). We categorized all hardwood trees as fire-tolerant oaks (FTO) or fire-sensitive hardwoods (FSH; Table 1) and summarized the stem count of trees in both categories at each plot (Table 2). The

Table 2
Summary (mean, standard deviation, and range) of response and explanatory variables used to model abundance of fire-tolerant oaks and fire-sensitive hardwoods counted at 307 inventory plots (0.04 ha). Type distinguishes between numerical (N) and categorical (C) variables. Fort Bragg Military Installation, North Carolina, USA, 2018.

	Type	$\bar{X}$ ± SD	Range
Response variable			
Fire-tolerant oak (stems)	N	5.10 ± 6.94	0–40
Fire-sensitive hardwood (stems)	N	1.03 ± 3.09	0–30
Explanatory variable			
Aspect (∘)	N	169.35 ± 106.06	0–360
Distance to firebreak (m)	N	69.34 ± 50.51	11.74–257.54
Dormant fires (count)	N	1.26 ± 1.20	0.00–6.00
Elevation (m)	N	92.26 ± 18.47	52.73–140.81
Fire return interval (years)	N	3.66 ± 1.02	2.15–9.33
Growing fires (count)	N	6.85 ± 2.09	1.00–13.00
Pine basal area (m^2/ha)	N	2.18 ± 1.27	0.00–6.39
Slope (%)	N	5.72 ± 3.21	0.54–16.11
Soil texture	C	–	sand
		–	loamy sand
Topographic Position Index	C	–	lower
		–	middle
		–	upper

number (count) of FTO and FSH present within the bounds of 0.04-ha plots served as the response variables. In addition, we used 10-factor prisms to quantify pine basal area at each plot. With the exception of pine basal area, all independent variables were collected using ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA; Table 2).

We used a LiDAR-derived digital elevation model (DEM) to calculate elevation (m), slope (%), and aspect (0–360°) in ArcGIS (Arcmap v. 10.5; ESRI, Redlands, CA, USA); aspect was transformed using a cosine transformation (Beers et al., 1966; Addington et al., 2015b). We used the Land Facet Tools ArcMap extension (Arcmap v. 10.5; ESRI, Redlands, CA, USA; Jenness et al., 2013) to categorize the DEM into a 3-category topographic position index (upper, mid, and lower). Soil texture was obtained from the SSURGO database (Soil Survey Staff, NRCS, 2018). Rather than using specific soil series, we categorized all soils into broader texture categories of "sand" or "loamy sand" (Gilliam et al., 1993; Addington et al., 2015b). We used Fort Bragg's prescribed fire records from 1991 to 2018 to determine number of total fires, dormant-season fires, and growing-season fires at each plot location. The cut-off date used by Fort Bragg to distinguish between growing-season and dormant-season fires varied by year depending on leaf-out and flowering dates observed for dominant trees and shrubs at the time of each fire, but dormant-season fires typically occurred early-January to mid-March, and growing-season fires typically occurred between mid-March and late-June. The number of years elapsed since the beginning of Fort Bragg's current fire management program (28 yr) was divided by the total number of fires to calculate the average fire return interval at each plot location. We used Fort Bragg's shapefile of roads and firebreaks to calculate the proximity to firebreaks at the center of each plot; we log-transformed distance to firebreaks to control for skewedness caused by extreme values. We scaled and standardized all other continuous covariates by subtracting the mean and dividing by the standard deviation.

2.3. Statistical analysis

We assessed pairwise correlations between all continuous independent variables using Pearson's correlation coefficients with a conservative cut-off of $\pm \mid 0.6 \mid$. We then used variance inflation factors with a cut-off of 3 to assessed multi-collinearity among all variables. If a pair-wise correlation coefficient exceeded the cut-off threshold, it was not included in a model with the variable with which it was correlated, and if one or more independent variables demonstrated high multi-collinearity by exceeding the cut-off threshold, we eliminated the variable with the highest VIF until no multi-collinearity was observed.

We used generalized linear models (GLM) to assess the important predictors of abundance for FTO and FSH abundance. A preliminary analysis using Poisson GLMs indicated a significant amount of overdispersion in models, so we used negative binomial GLMs using the 'MASS' package in R (Venables and Ripley, 2002; R Core Team, 2018). Negative binomial GLM routines are widely understood to handle overdispersed count data that are not normally distributed (Burnham and Anderson, 2002; Zuur et al., 2009; Miyamoto et al., 2018). We used chi-square goodness-of-fit to calculate dispersion statistics for the global models of both FTO and FSH (Zuur et al., 2009; Hilbe and Robinson, 2013). A dispersion statistic (ϕ) > 1 is a sign of overdispersion and may indicate lack-of-fit (Burnham and Anderson, 2002; Zuur et al., 2009; Hilbe and Robinson, 2013). In models with overdispersion, we dealt with the potential lack-of-fit by multiplying the standard error by the variance inflation factor ($\sqrt{\phi}$; Anderson et al., 1994; Lindsey, 1999; Burnham and Anderson, 2002; Zuur et al., 2009). We developed 19 *a priori* models and ranked them according to Akaike information criteria (AIC). If overdispersion was detected, we re-ranked the candidate set with quasi Akaike information criteria (QAIC [Burnham and Anderson, 2002]).

A preliminary analysis indicated the number of growing-season fires was correlated with fire return interval and the number of dormant-season fires ($R = -0.76$, $R = -0.53$, respectively); therefore, we did not use the number of dormant-season fires in any models, and no models containing fire return interval contained the number of growing-season fires. First, we fit null models where abundance of FTO and FSH was constant at all sites (Appendix A, Table A.1, Model 17). Next, we developed 11 hypothetical models for abundance of FTO and FSH which included combinations of independent variables we expected to influence abundance (e.g., distance from firebreaks, elevation, fire return interval, growing-season fires, pine basal area, slope, soil, and topographic positions; Appendix A, Table A.1). All combinatory models contained distance from firebreaks and pine basal area because of their reported importance in predicting hardwood abundance throughout the longleaf pine range (Jacqmain et al., 1999; Addington et al., 2015a, b) and on Fort Bragg (Lashley et al., 2014). Also, we included one model containing only topographic variables, one containing only environmental conditions, and two sub-global models – one with all variables except the number of growing season fires, and one with all variables except the fire return interval (Appendix A, Table A.1, Models 15 and 16, respectively).

2.4. Model inference

We used AIC/QAIC to rank the *a priori* model set, and we chose the top model for FTO and FSH abundance based on the lowest AIC/QAIC (Burnham and Anderson, 2002). We considered any model within 2ΔAIC/QAIC of the model with the lowest AIC/QAIC and assessed all competitive models for uninformative parameters and parsimony (Burnham and Anderson, 2002; Arnold, 2010). If a more parsimonious model was within 2ΔAIC/QAIC of the AIC-best model, it was selected as the final model. If a more complex model was within 2ΔAIC/QAIC of the AIC-best model, we calculated 85% confidence intervals for each coefficient (Arnold, 2010); if the confidence intervals of additional parameters overlapped zero, we categorized the parameter as uninformative and selected the AIC-best model as our final model. After selecting the final models of both FTO and FSH, we calculated 85% and 95% confidence intervals to examine the statistical support for evidence of a strong covariate effect for every coefficient in the final model. If neither 95% confidence intervals nor 85% confidence intervals overlapped zero, we considered this strong evidence of a covariate effect. If the 95% confidence interval overlapped zero, but the 85% confidence interval did not, we considered this weak evidence of a covariate effect. Finally, if the 95% confidence interval crossed zero, we considered that covariate effect to have no statistical support and refrained from making inferences related to that parameter.

3. Results

3.1. Fire-tolerant oaks

Fire-tolerant oaks were present at 196 of the 307 plots (63.8%), and stem counts ranged from 1 to 40 stems (Table 2). Across all plots, we counted 1566 stems of FTO species, which accounted for 83.2% of the total number of hardwood stems counted (i.e., 1882), and plots averaged 5.10 ± 6.94 stems (Table 2). Turkey oak, blackjack oak, and sand post oak were the most abundant FTO detected, with 746 (39.7%), 463 (24.6%), and 193 (10.3%) total stems, respectively (Table 1). Bluejack oak and post oak were the least common FTO species across sites, with 50 (2.7%) and 44 (2.3%) total stems, respectively (Table 1). We did not identify overdispersion in the negative binomial FTO model ($\phi = 0.96$, $X^2 = 283.31$, df = 295), and we ranked models using AIC.

The top model for FTO abundance included linear effects of distance from firebreaks, percent slope, pine basal area, and fire return interval (Table 3). Four models were within 2ΔAIC of the top model; however, these models were more complex than the AIC-best model, and the additional parameters were deemed uninformative. For distance from firebreaks, neither the 95% confidence interval, nor the 85% confidence

Table 3
The number of parameters (K), AIC, ΔAIC, model weight (ω), and negative loglikelihood (-LogLik) for all models of fire-tolerant oak abundance. Fort Bragg Military Installation, North Carolina, USA, 2018.

Model	K	AIC	ΔAIC	ω	-LogLik
FB + FRI + Pine + Slope	6	1530.6	0.0	0.3	−759.3
FB + Grow + Pine + Slope	6	1531.1	0.5	0.2	−759.6
FB + FRI + Pine + Slope + Soil	7	1532.6	2.0	0.1	−759.3
FB + Grow + Pine + Slope + Soil	7	1533.1	2.5	0.1	−759.6
FB + Grow + Pine + Soil	6	1533.6	3.0	0.1	−760.8
FB + FRI + Pine + Slope + TPI	8	1534.4	3.8	0.0	−759.2
FB + FRI + Pine + TPI	7	1534.9	4.3	0.0	−760.5
FB + Grow + Pine + Slope + TPI	8	1534.9	4.3	0.0	−759.5
FB + FRI + Elevation + Pine + Soil	7	1535.0	4.3	0.0	−760.5
FB + Grow + Pine + TPI	7	1535.3	4.7	0.0	−760.7
FB + Grow + Elevation + Pine + Soil	7	1535.4	4.8	0.0	−760.7
Sub-Global: FRI	11	1540.0	9.4	0.0	−759.0
Sub-Global: Grow	11	1540.6	10.0	0.0	−759.3
Environmental	9	1540.9	10.3	0.0	−761.5
Null	2	1585.1	54.5	0.0	−790.5

FB – Distance to firebreaks, Pine – pine basal area, Soil – soil type, Grow – number of growing-season fires, FRI – fire return interval, Slope – percent slope, TPI – topographic position index

Table 4
Coefficients, 85% confidence interval, and 95% confidence interval of parameter estimates for covariates in the top-ranked model of fire-tolerant oak abundance. Fort Bragg Military Installation, North Carolina,

Parameter	β	SE	85% CI		95% CI	
Intercept	2.23	0.40	1.65	2.81	1.45	3.02
Dist. Firebreak [a]	−0.22	0.10	−0.36	−0.07	−0.41	−0.02
Pine BA [a]	−0.72	0.09	−0.85	−0.59	−0.89	−0.54
FRI [b]	0.06	0.08	−0.06	0.18	−0.10	0.22
Slope [c]	0.14	0.08	0.03	0.26	−0.02	0.30

[a] Parameters with strong statistical support.
[b] Parameters without statistical support.
[c] Parameters with weak statistical support.

interval overlapped zero, and we concluded there was strong statistical support for effect of distance from firebreaks (Table 4). FTO abundance decreased as distance from firebreaks increased (Fig. 2a). Also, there was strong support for pine basal area as a negative predictor of FTO abundance as neither confidence interval overlapped zero (Table 4), and FTO abundance decreased as pine basal area increased (Fig. 2c). Additionally, there was weak evidence for the effect of slope on FTO abundance as the 95% confidence interval overlapped zero, but the 85% confidence interval did not (Table 4). FTO abundance was greater on steeper slopes (Fig. 2b). Although fire return interval was present in the top model, both the 95% and 85% confidence intervals overlapped zero (Table 4), and we concluded there was no support for the fire return interval as a predictor of FTO abundance, and we did not make inferences regarding the effect of fire return interval on FTO abundance.

3.2. Fire-sensitive hardwoods

Fire-sensitive hardwoods were present at 76 of the 307 plots (24.8%), and at plots where FSH were present, stem counts ranged from 1 to 30 stems (Table 2). Across all plots, we counted 316 stems of FSH species, which accounted for 16.8% of the total number of stems counted (i.e., 1882). Plots averaged 1.03 ± 3.09 FSH stems (Table 2). Hickories, sweetgum, and flowering dogwood were the FSH species that occurred most frequently across all plots, with 73 (3.88%), 65 (3.46%), and 52 (2.8%) total stems, respectively (Table 1). Butternut, red maple, and black cherry were the least common FSH species, with 2 (0.2%), 1 (0.1%), and 1 (0.1%) total stems, respectively (Table 1). There was overdispersion in the FSH model ($\phi = 1.59$, $X^2 = 467.378$, df = 295), and we ranked models using QAIC and inflated the standard errors prior to calculating confidence intervals and making predictions.

The top model for FSH abundance included linear effects of distance from firebreaks, the number of growing-season fires, elevation, pine basal area, and soil texture (Table 5). There were two models within 2ΔQAIC of the top model (Table 5). The second ranked model included fire return interval, but we deemed this parameter uninformative. Moreover, the third ranked model was less complex than the QAIC-best model, but the additional parameter in the top ranked model (i.e. elevation) was deemed informative. For distance from firebreaks, the 85% and 95% confidence intervals crossed zero, and thus we concluded that there was no statistical support for the covariate effect (Table 6). Initially, there was strong evidence for the effect of the number of growing-season fires on FSH abundance, but after inflating the standard error by the variance inflation factor ($\sqrt{\phi}$), the 85% confidence interval overlapped zero, and we concluded there was weak evidence to suggest that the number of growing-season fires influenced FSH abundance (Table 6). The number of FSH decreased with a greater number of growing-season fires (Fig. 3a). Furthermore, there was weak evidence in support of elevation as a predictor of FSH abundance (Table 6). FSH abundance decreased as elevation increased (Fig. 3b). There was strong support for pine basal area as a predictor of FSH abundance (Table 6). FSH abundance decreased with greater pine basal area (Fig. 3c).

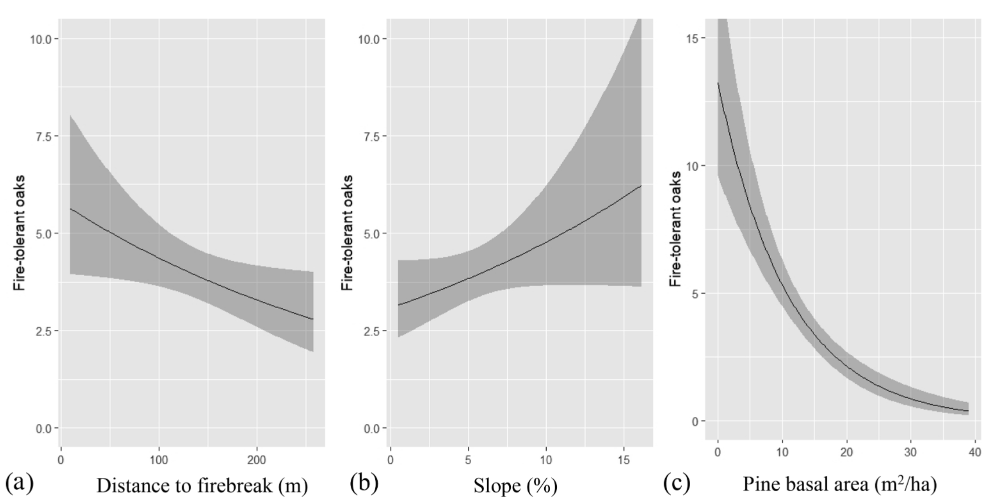

Fig. 2. Fire-tolerant oak abundance and 95% CI in relation to predictors in the top model (a) distance to firebreaks, (b) slope, and (c) pine basal area. 95% Confidence Intervals. Fort Bragg Military Installation, North Carolina, USA, 2018.

Table 5
The number of parameters (K), QAIC, ΔQAIC, model weight (ω), and negative log-likelihood (-LogLik) for all models of fire-sensitive hardwood abundance. Fort Bragg Military Installation, North Carolina, USA, 2018.

Model	K	QAIC	ΔQAIC	ω	-LogLik
FB + Grow + Elevation + Pine + Soil	7	394.9	0	0.5	−302.8
FB + FRI + Elevation + Pine + Soil	7	396.6	1.7	0.2	−304.2
FB + Grow + Pine + Soil	6	396.8	1.9	0.2	−305.9
FB + Grow + Pine + Slope + Soil	7	398.8	3.9	0.1	−305.9
Environmental	9	399.5	4.6	0.0	−303.3
Sub-Global: Grow	11	400.7	5.8	0.0	−301.0
FB + FRI + Pine + Slope + Soil	7	402.6	7.7	0.0	−308.9
Sub-Global: FRI	11	402.7	7.8	0.0	−302.7
FB + Grow + Pine + TPI	7	412.3	17.4	0.0	−316.7
FB + Grow + Pine + Slope	6	413.9	19	0.0	−319.5
FB + Grow + Pine + Slope + TPI	8	414.3	19.4	0.0	−316.6
FB + FRI + Pine + TPI	7	415.5	20.6	0.0	−319.2
FB + FRI + Pine + Slope	6	415.8	20.9	0.0	−321.0
FB + FRI + Pine + Slope + TPI	7	415.8	20.9	0.0	−319.4
Topography	7	426.2	31.4	0.0	−327.7
Null	2	431.1	36.2	0.0	−339.5

FB – Distance to firebreaks, Pine – pine basal area, Soil – soil type, Grow – number of growing-season fires, FRI – fire return interval, Slope – percent slope, TPI – topographic position index

Table 6
Coefficients, 85% confidence interval, and 95% confidence interval of parameter estimates for covariates in the top-ranked model of fire-sensitive hardwood abundance. Overdispersion corrected for by inflating standard error by $\sqrt{1.59}$. Fort Bragg Military Installation, North Carolina, USA, 2018.

Parameter	β	SE	85% CI		95% CI	
Intercept	0.60	0.93	−0.74	1.94	−1.22	2.42
Dist. firebreak [a]	−0.44	0.52	−1.19	0.31	−1.46	0.58
Growing fires [b]	−0.27	0.19	−0.54	−0.01	−0.64	0.10
Elevation [b]	−0.36	0.20	−0.64	−0.07	−0.75	0.03
Pine BA [c]	−0.93	0.23	−1.26	−0.60	−1.38	−0.48
Soil (sand) [c]	−1.98	0.46	−2.64	−1.32	−2.88	−1.09

[a] Parameters without statistical support
[b] Parameters with weak statistical support
[c] Parameters strong statistical support

Finally, there was evidence of a strong covariate effect of soil texture (Table 6). Plots that were in areas of loamy sand soils had more FSH trees than plots on sandy soils (Fig. 3d).

4. Discussion

The two guilds of hardwoods demonstrated mostly differing relationships with the variables related to site conditions and fire history. Fire-tolerant oaks were most abundant on xeric sites, and no aspects of fire history were important for predicting abundance for this guild. Fire-sensitive hardwoods were most abundant on mesic sites, and fire seasonality was important for predicting abundance for these species. Abundance of FSH was negatively influenced by the number of burns conducted during the growing-season; results of previous studies of this relationship have been mixed, with some reporting that growing-season fires negatively influenced hardwood abundance and yielded greater fire-related mortality than dormant season fires (Waldrop et al., 1992; Boyer, 1993; Streng et al., 1993; Glitzenstein et al., 1995), whereas other studies have reported little effect of fire season on hardwoods (Addington et al., 2015a, b, Whelan et al., 2018). Pine basal area was present in the best models of abundance for both FTO and FSH guilds, which highlights the importance of pine basal area management as a predictor of upland hardwood abundance and distribution in frequently burned, longleaf pine communities.

Our results indicate that FTOs are more likely to be present on xeric sites, and that percent slope is a more important predictor of FTO abundance than soil characteristics and other aspects of topography associated with xeric conditions (e.g., aspect, elevation, and topographic position). Fire-tolerant oak species (e.g., turkey oak, blackjack oak, and sand post oak) have well-documented affinities for xeric and sub-xeric site conditions and accounted for the majority (89.53%) of the hardwood tree species we encountered (Peet and Allard, 1993; Jacqmain et al., 1999; Sorrie et al., 2006; Carr et al., 2010). Many of the FTO species, especially turkey oak, are common on xeric sites in the Sandhills (Peet and Allard, 1993; Greenberg and Simons, 1999; Sorrie et al., 2006; Carr et al., 2010). Xeric conditions occur frequently on steeper slopes because of decreased soil moisture caused by greater amounts of run-off and the low water holding capacity of the courser soil textures present (Jenny, 1994; Addington et al., 2015b). Steep slopes could further promote the persistence of mature FTO stems by decreasing fire-induced mortality through increased rates of fire spread, decreased residence times, and increased patchiness due to sparser fuels – depending on ignition conditions, firing techniques, and fuel characteristics (Rothermel, 1983; Glitzenstein et al., 1995; Jacqmain et al., 1999; Addington et al., 2015b).

The influence on fire behavior is the most plausible explanation for the importance of distance to firebreaks for predicting FTO abundance. Areas near firebreaks allow FTO species to achieve greater densities because fires burn with less intensity proximal to ignition sources (Lashley et al., 2014). It is likely that over long time scales, xeric conditions act both independently and in concert with proximity to firebreaks to influence fire behavior such that steep slope areas proximal to firebreaks are less likely to experience intense fires capable of damaging FTO species. Our results indicate that managers concerned with retaining upland hardwood inclusions likely would achieve success on steep slopes and areas adjacent to firebreaks; conversely, these areas can be targeted by managers seeking to reduce upland hardwood cover in longleaf pine communities.

Fire-sensitive hardwood species were more abundant on sandy loam soils and at lower elevations due to the better growing conditions and how local fire behavior is affected by edaphic conditions. On Fort Bragg, lower elevations and sandy loam soils typically were associated with mesic ecotones adjacent to riparian corridors (Sorrie et al., 2006; Just et al., 2016), and the conditions in these mesic ecotones interact with fire behavior to drive FSH abundance. For example, riparian zones act as natural firebreaks (Just et al., 2016), creating heterogeneity in fire behavior (e.g., patchiness and intensity) that may positively affect FSH abundance. Although we did not document support for fire return interval as predictor of FSH abundance, the number of growing-season fires was an important predictor. Previous research has shown that growing-season burning causes more hardwood mortality than dormant-season fires (Boyer, 1990; Streng et al., 1993; Glitzenstein et al., 1995). We suggest growing season fire negatively influenced FSH abundance because these fires burn with greater intensity and more continuity in the low-lying areas and sandy loam soils where FSH species tend to persist. The greater intensity and increased continuity of growing season fire occurs due to higher ambient temperatures and decreased fuel moisture during the late-spring and early-summer; when these factors are combined with the increased vulnerability to fire-induced mortality during the growing season, there is decreased survival and abundance of FSH species in low lying areas burned during the early growing season.

Pine basal area was an important predictor of abundance for both guilds of hardwoods, a relationship previously documented (McGuire et al., 2001; Knapp et al., 2014; Addington et al., 2015a, b; Whelan et al., 2018). Researchers have suggested two mechanisms by which areas with greater pine basal area or canopy cover may negatively influence hardwood tree abundance. Hardwoods may be less abundant in areas with high levels of pine basal area because of decreased light availability and greater competition for space, water, and nutrients (McGuire et al., 2001; Knapp et al., 2014; Addington et al., 2015b). Also, areas high in pine basal area result in greater amounts of litter

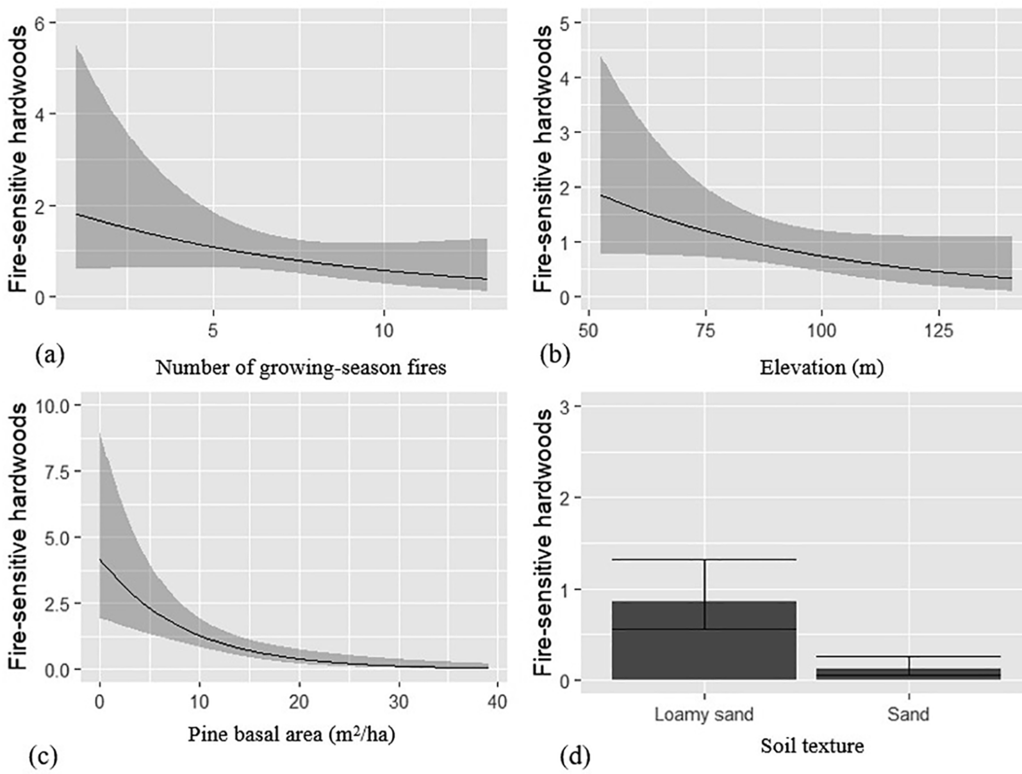

Fig. 3. Fire-sensitive hardwood abundance and 95% CI in relation to predictors in the top model (a) number of growing-season fires, (b) elevation, (c) pine basal area, and (d) soil texture. Fort Bragg Military Installation, North Carolina, USA, 2018.

composed of flammable pine needles that can increase fuel loads and continuity, which results in more intense fires which may burn more contiguously (Platt et al., 2016), and thus increase fire-related mortality (Addington et al., 2015b, Whelan et al., 2018). Although we showed the number of growing-season fires was an important negative predictor of FSH abundance, we did not detect support for fire history variables as predictors of FTO abundance. These results indicate that pine-mediated fire behavior potentially influences FSH abundance, but competition for light and other resources, rather than fire history, drive the relationship between pine basal area and FTO abundance. Hence, following thinning to reduce pine overstory, FSH species may be less susceptible to fire due to decreased fire intensity related to less fuel composed of pine needles, and FTO may be released to achieve fire-resistant sizes by increasing light, water, and space availability associated with less pine competition. However, with repeated growing season burning and the subsequent establishment of robust ground covers, pine basal area could become less influential over time. More specifically, increased cover of herbaceous species (e.g., wiregrass) may increases the intensity and contiguity of burns, thus leading to greater fire-related hardwood mortality.

There are a couple of explanations for why we did not detect support for fire return interval as an important predictor of hardwood tree abundance. Most importantly, landscape-level homogeneity in fire return interval across Fort Bragg may have limited our ability to test fire return interval as a predictor of FTO and FSH abundance. On Fort Bragg, there was little variation in fire return interval ($\bar{x}$ = 3.66 ± 1.02 years), and the majority of sample plots had intervals between 2 and 4.5 years (83.1%). Another explanation may be related to the possibility that fire return interval exerted its influence on community structure early in the course of frequent fire reintroduction. Over the long-term, managing with frequent, recurrent fire likely caused plant communities to segregate into the respective landscape positions that enable them to persist in the presence of frequent fire, and thus more fire-sensitive hardwood species become restricted to mesic areas that are prone to burning less intensely and possibly less frequently; conversely, more fire-tolerant species may be able to occupy steep slopes, ridges, and areas near firebreaks because of the ways in which these areas influence fire behavior.

Although we did not determine that fire return interval was an important predictor of FTO and FSH abundance, season of burn had an influence on FSH abundance. The reported effects of fire season on mature hardwood dynamics vary, with some studies reporting greater hardwood stem mortality or decreased abundance in response to growing-season fire (Boyer, 1990; Streng et al., 1993; Glitzenstein et al., 1995), increased hardwood stem densities in response to dormant-season burning (Boyer, 1993), or no effect of fire season (Waldrop et al., 1992; Brockway and Lewis, 1997; Addington et al., 2015a, b). Although the results of our FTO analysis are inconsistent with Boyer (1990), their grouping of all oaks as a single response variable makes comparisons difficult regarding the effects of repeated growing-season burning. Furthermore, our results contradict those reported by Streng et al., (1993) and Glitzenstein et al., (1995), who reported that trees we categorized as FTO experienced reduced survival, recruitment, and density in response to growing-season fire; however, the relationships in FSH species were similar in that FSH abundance was negatively influenced by the number of growing-season burns.

The differences we observed between important predictors of FTO and FSH highlight the need to consider species or species guilds independently when constructing management plans. FSH species, whether mesophytic or tolerant of a broader range of site conditions, become relegated to mesic areas where fires burn more heterogeneously and with less intensity and frequency. Fire return interval was not an important predictor of tree abundance for FTO and FSH species, which may indicate that coarse fire history metrics may be less important than individual fire behavior, or that the observable effects of fire return interval on hardwood distribution are exerted early in a fire restoration program. We suggest that future investigations account for the influence of individual fires and long-term trends in fire history when studying the effects of fire on hardwood distributions in upland longleaf pine communities.

5. Conclusions

Our investigation was not intended to challenge the widespread understanding that the early stages of restoring fire-suppressed longleaf pine communities require extensive hardwood reduction. However, managers should have realistic expectations regarding hardwood dynamics; efforts to eradicate hardwoods are difficult, time consuming, and costly (Provencher et al., 2001; Hiers et al., 2014). Additionally, those involved in long-term management should recognize hardwoods, especially FTO, as critical components of upland longleaf pine communities (Peet and Allard, 1993; Greenberg and Simons, 1999; Carr et al., 2010; Hiers et al., 2014, 2016). We suggest that future management should strive to view the landscape from the perspective of Fill et al., (2015), who described longleaf pine ecosystems as a dynamic mosaic of longleaf pine dominated savannas, woodlands, and grasslands interspersed with hardwood patches of variable extents and age distributions. We suggest incorporating strategies that support development of natural vegetation-fire feedback mechanisms such as increasing the size of burn blocks (e.g., reducing firebreak systems), using firing techniques that promote burn patchiness, and developing fire prescriptions that incorporate the range of historical variability (e.g., variation in fire frequency, season, and extent). For managers seeking to promote small amounts of FTO in upland longleaf pine communities, or to allow for the persistence of FTO, the greatest success would be achieved on steeper slopes and near firebreaks. FSH species are relegated to areas at low elevation with loam soils that have experienced few growing season fires and hence may be of lesser concern to managers interested in restoring upland longleaf pine communities.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The United States Department of Defense, Fort Bragg Military Installation, and the Fisheries, WIldlife, and Conservation Biology Program at North Carolina State University provided financial support for the research.

Appendix A

See Table A1.

Table A1
Names and formulas of *a priori* models used to predict abundance of fire-tolerant oaks and fire-sensitive hardwoods counted at 307 inventory plots (0.04 ha). Fort Bragg Military Installation, North Carolina, 2018.

Model	Formula
M1	Dist. firebreak + FRI + Pine BA + Slope + Soil text.
M2	Dist. firebreak + FRI + Elevation + Pine BA + Soil text.
M3	Dist. firebreak + FRI + Pine BA + Slope
M4	Dist. firebreak + FRI + Pine BA + TPI
M5	Dist. firebreak + FRI + Pine BA + Slope + TPI
M6	Dist. firebreak + Growing fire + Pine BA + Slope + Soil text.
M7	Dist. firebreak + Growing fire + Elevation + Pine BA + Soil text.
M8	Dist. firebreak + Growing fire + Pine BA + Soil text.
M9	Dist. firebreak + Growing fire + Pine BA + Slope + TPI
M10	Dist. firebreak + Growing fire + Pine BA + TPI
M11	Dist. firebreak + Growing fire + Pine BA + Slope
M12	Aspect + Elevation + Slope + TPI
M13	Aspect + Elevation + Slope + Soil text. + Pine BA + TPI
M17	Null
M18	Aspect + Dist. firebreak + Elevation + FRI + Slope + Soil text. + Pine BA + TPI
M19	Aspect + Dist. firebreak + Elevation + Growing fire + Slope + Soil text. + Pine BA + TPI

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