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The use of witness trees as pyro-indicators for mapping past fire conditions

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ABSTRACT

Understanding and mapping presettlement fire regimes is vitally important for ecosystem restoration, helping ensure the proper placement of fire back into ecosystems that formerly burned. Witness trees can support this endeavor by serving as pyro-indicators of the past. We mapped fire-adapted traits across a landscape by categorizing trees into two classes, pyrophiles and pyrophobes, and applying this classification to a geospatial layer of witness-tree points centered on the Monongahela National Forest, West Virginia. A pyrophilic percentage was calculated for each point and spatially extrapolated via ordinary kriging to form a continuous geospatial cover. Regression analyses showed pyrophilic percentage was significantly related to a number of key environmental factors and changed along an elevation gradient from low, dry valleys (high pyrophilic percentage) to high, wet mountaintops (low pyrophilic percentage). This approach represents a significant advancement through the direct use of witness trees to depict past fire regimes applicable to both Public Land Survey and metes-and-bounds records.

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1. Introduction

Ecosystem restoration is predicated on documenting past compositions, structures, and spatial patterns within and across landscapes (SER, 2004). Even though vegetation characteristics are crucial for establishing reference conditions and restoration goals, the underlining disturbance regimes that profoundly shape ecosystems and vegetation expression are often overlooked. Indeed, re-establishing former disturbance regimes, i.e. returning natural flows/hydrologic pulses back to rivers (Postel and Richter, 2003) or fire back into pyrogenic ecosystems (Nowacki and Abrams, 2008), is vitally important. Since many terrestrial ecosystems are disturbance dependent and have been negatively affected by the disruption/discontinuance of former disturbances (Cowell, 1998; Whitney, 1987; Bond et al., 2004; Bowman et al., 2009), land managers have shifted towards emulating natural disturbance regimes for ecosystem restoration and sustainability (Seymour et al., 2002; North and Keeton, 2008; Long, 2009). By restoring fundamental disturbance processes, the evolutionary environment and basic ecological functions can be re-established, thus leading to the return of historic vegetation conditions.

Direct information for determining presettlement fire regimes in the eastern United States is scarce. Original forests have been greatly modified by European settlement activities, especially through exploitative logging, accidental and deliberate burning, land clearing, and pasturage (Williams, 1990; Whitney, 1994; MacCleery, 1996; Lewis, 1998). This transformation has been so complete that remaining "virgin" forests are few, scattered, and largely unrepresentative of past vegetation types (Nowacki and Trianosky, 1993). Likewise, older trees that may have recorded fire history in their rings are mostly gone. Moreover, even if they did exist, it is questionable whether past fire regimes of low to moderate intensity would be readily detectable through fire scars (McEwan et al., 2007). Vast opportunities exist with paleoecological data (stratigraphic charcoal), however their spatial distribution is geographically unbalanced (skewed to areas with high concentrations of lakes, ponds, and wetlands) with large voids across the east (see Fig. 1 of Hart and Buchanan, 2012). Moreover, charcoal interpretations are imperfect (Higuera et al., 2005) and the high resolution required from the charcoal record for concise fire regime reconstruction is usually not available (Clark, 1988), although there has been marked improvement in these regards (Power et al., 2008). Radiocarbon-dating of soil and cave-alluvial charcoal looks promising for reconstructing past fire regimes, but research is only in its infancy with few studies to date (Talon et al., 2005; Hart et al., 2008; Fesenmayer and Christensen, 2010; Springer et al., 2010). In the absence of such direct evidence, inferences from indirect information sources may be best for scientists and land managers seeking to understand past disturbance regimes.

The recognition that disturbance played a key role in determining past vegetation compositions, structures, and patterns has

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spurred efforts to map fire regimes for restoration purposes (Wright and Bailey, 1982; Pickett and White, 1985; Engstrom et al., 1999). In the United States, pioneering works by Frost (1998) and Schmidt et al. (2002) have been subsequently improved upon by others employing a variety of approaches (Guyette et al., 2005, 2012; Nowacki and Abrams, 2008). The need for higher resolution maps for land management have led to an increasingly sophisticated array of maps combining soils, topography, human history, remnant vegetation, landscape concepts, and local knowledge (Cleland et al., 2004; Schulte and Mladenoff, 2005; Bailey et al., 2007; Thomas-Van Gundy et al., 2007; Stambaugh and Guyette, 2008). This study represents a continuation of these recent advancements, specifically through the use of witness trees as pyro-indicators.

Although many historical datasets lend themselves to establishing reference conditions (Whitney, 1994; Egan and Howell, 2001), witness-tree databases are among the best. This is particularly so for Public Land Survey (PLS) records (Bourdo, 1956; Delcourt, 1976; Schwartz, 1994; Delcourt and Delcourt, 1996; He et al., 2000; Schulte and Mladenoff, 2001; Manies et al., 2001; Black et al., 2002; Bollinger et al., 2004; Anderson et al., 2006; Kronenfeld and Wang, 2007), which provide systematic and detailed witness-tree information (species, size, and distance) for reconstructing past compositions (species frequency) and structures (stand density and basal area). By coupling PLS information with more recent inventories, changes in vegetation conditions can be readily detected (Whitney, 1987; Iverson, 1988; Fralish et al., 1991; White and Mladenoff, 1994; Zhang et al., 2000; Rhemtulla et al., 2007). Although reconstructing historic disturbance regimes has been a minor focus of witness-tree research, literature has been progressively building (Lorimer, 1977; Canham and Loucks, 1984; Whitney, 1986; Seischab and Orwig, 1991; Zhang et al., 1999; Cleland et al., 2004; Schulte et al., 2004; Schulte and Mladenoff, 2005). Most efforts focus on line notes, which denote surveyor entry and exit of disturbed areas (primarily wind- and fire-based), to estimate disturbance attributes such as size, frequency, and return interval.

In the far eastern United States (original 13 colonies), witness-tree data were recorded via the metes-and-bounds system of land measurement. Unfortunately, the manner in which witness-tree data were derived greatly limits their ecological use (Kronenfeld and Wang, 2007). Thus, alternatives are needed to characterize past disturbance regimes using witness trees from metes-and-bounds surveys. To overcome inherent limitations of this survey method, we offer a novel solution where witness tree species are classified by fire relations (pyrophilic or pyrophobic) based on ecological literature. From this classification, a pyrophilic percentage is calculated at each witness-tree point and these percentages spatially extrapolated via ordinary kriging to form a continuous surface. From this pyrophilic percentage cover, we created a new fire adaptation map and compared it a previously published rule-based model (Thomas-Van Gundy et al., 2007).

2. Methods

2.1. Study area

The spatial extent of this study spans the proclamation boundary for the Monongahela National Forest, which covers about 710,000 ha (Fig. 1). National Forest System lands comprise about 371,000 ha of this area; the remainder is held in State, private, or other federal ownership. The study area includes portions of two ecological sections with different geomorphologies and climates: the Allegheny Mountains and Northern Ridge and Valley (Cleland et al., 2005), with most of the study area lying in the former section.

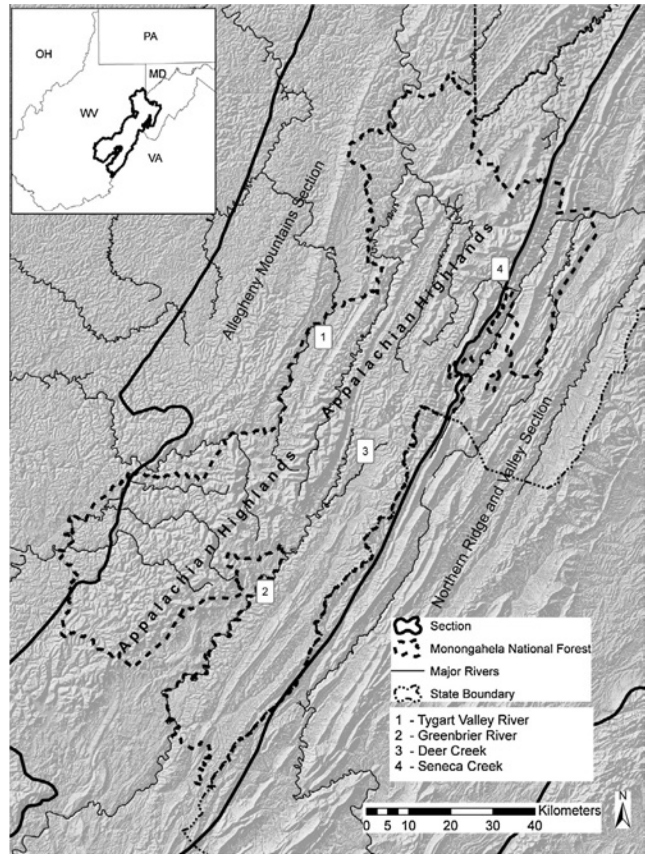

Fig. 1. Study area location showing ecological sections, major rivers, and selected reference points mentioned in the text.

The Allegheny Mountains Section has a wet and cool climate, with 100–138 cm of precipitation per year (about 20% as snow; 30% at higher elevations), an annual average temperature of 8–11 °C, an average annual maximum temperature of 14.5–17 °C, an average annual minimum temperature of 2–4 °C, and a growing season of 126–155 days in the study area (Cleland et al., 2005). The vegetation of the Allegheny Mountains is strongly influenced by elevation, forming four broad zones: oak, mixed mesophytic, northern hardwoods, and red spruce. The lowest elevations (valleys and foothills) are dominated by oaks, which associate with sycamore (*Platanus occidentalis* L.), river birch (*Betula nigra* L.), and various mesophytes along riparian corridors and in floodplains. Upslope, the vegetation transitions into mixed mesophytic forests, which include yellow-poplar (*Liriodendron tulipifera* L.), basswood (*Tilia americana* L.), white ash (*Fraxinus americana* L.), sugar maple (*Acer saccharum* Marsh.) and northern red oak (*Quercus rubra* L.). The rich, mesic cove hardwoods are diagnostic of this group. The northern hardwood group is found on upper slopes and ridge tops and features sugar maple, yellow birch (*Betula alleghaniensis* Britt.), American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and black cherry (*Prunus serotina* Ehrh.). Red spruce (*Picea rubens* Sarg.) forests occur at the highest elevations (above 1000 m) often mixing with northern hardwoods.

Much of the Northern Ridge and Valley Section lies in the rain shadow of the Allegheny Mountains and supports vegetation reflective of drier conditions (Abrams and McCay, 1996; McCay et al., 1997). Annual precipitation ranges from 100–107 cm, although it may be as high as 152 cm near the Allegheny Plateau (Cleland et al., 2005). Annual temperature ranges from 10–12 °C, with an average annual maximum temperature of 17–19 °C, an average annual minimum temperature of 4–5 °C, and the growing season ranges from 149–170 days in the study area (Cleland et al., 2005). In general, northern red oak and white oak (*Quercus alba* L.) occur on productive mesic sites, often intermixed with eastern white pine (*Pinus strobus* L.) on side slopes. Increases in scarlet (*Quercuscoccinea* Muenchh.) and black oak (*Quercusvelutina* Lam.) occur on progressively drier sites. On the driest sites, pitch (*Pinusrigida* Mill.), Table Mountain (*Pinuspungens* Lam.), or Virginia (*Pinusvirginiana* Mill.) pines predominate, either in pure stands or mixed with scrub oak (*Quercusilicifolia* Wangenh.) or other oak species.

2.2. Witness tree data

A geospatial database of approximately 22,000 witness trees representing the earliest deeds (1752–1899) was used as the basis for this study (Thomas-Van Gundy and Strager, 2012). Most corners were represented by 1 or 2 trees, ranging up to 6 trees (Table 1). Unlike early surveys in the Midwest, systematic grid surveys were uncommon in the original colonies including what is now the state of West Virginia. In the study area, land was surveyed by the metes-and-bounds method, which consisted of a series of bearings and distances associated with trees, posts, rock piles, or other natural features that marked corners. Trees used as the parcel corner or located close to the corner are called witness trees. Deeds or grants documenting transfer of ownership of a parcel of land also document tree species existing at the time of transfer through these witness trees (Abrams and Ruffner, 1995; Black and Abrams, 2001a,b; Rentch and Hicks, 2005; Whitney and DeCant, 2003; Thomas-Van Gundy and Strager, 2012).

A total of 49 different species or genera used as witness trees were categorized as pyrophilic or pyrophobic based on their known fire relations according to the literature (Table 2). A number of different traits were considered when classifying witness trees in this manner. Fire can be thought of as an herbivore with a broad diet (Bond and Keeley, 2005), shaping plant evolution since at least the late Cretaceous period (Keeley et al., 2011). Species evolve adaptations to the combination of climate, topography, and disturbance regimes within their range (Keeley et al., 2011). Disturbance regimes can be characterized using a number of parameters, including disturbance type, distribution, frequency (or related measures like return interval or rotation period), and magnitude (White and Pickett, 1985). For this analysis we focused on species traits adapted (or not) to a regime of frequent, low-to-moderate intensity surface fire, although many species may take advantage of site conditions created after a single fire (e.g. yellow birch, yellow-poplar, black cherry). For example, we consider red spruce to be pyrophobic because, with thin bark, no sprouting response, and non-serotinous cones, the species is poorly adapted to frequent fires of low or moderate intensity. Witness trees possessing traits for persistence under a fire regime of frequent, low-to-moderate intensity surface fires were assigned pyrophilic; those possessing fire-sensitive, mesophytic traits were assigned pyrophobic.

Table 1
Descriptive statistics of witness-tree point data from east-central West Virginia.

Category of witness tree point	No. in study area
No. of 1-tree points	7710
No. of 2-tree points	5451
No. of 3-tree points	1016
No. of 4-tree points	131
No. of 5-tree points	24
No. of 6-tree points	4
Total no. of points	14,336
No. of exclusively pyrophilic points	6329
No. of mixed points	2109
No. of exclusively pyrophobic points	5898
Total no. of points	14,336

2.3. Analyses

Once status for each species was determined, a pyrophilic percentage was calculated for each survey corner by dividing the number of pyrophilic trees by the total number of trees (pyrophobic and pyrophilic) and multiplying by 100. Corners comprised exclusively of pyrophobic or pyrophilic trees had percentages of 0 and 100 respectively. Based on previous work (Thomas-Van Gundy and Strager, 2012), witness trees listed as "pine" in one ecological subsection were likely red spruce, and thus changed prior to this analysis.

Ordinary kriging was used in ArcMap 10 (ESRI, 2010) to interpolate the pyrophilic percentage between points and create a continuous cover for the study area. Ordinary kriging was chosen as positive spatial autocorrelation found in the dataset (Thomas-Van Gundy and Strager, 2012) violated the stationarity assumption of universal kriging. Even though the distribution of pyrophilic percentage by points was not normal (ordinary kriging assumes a normal distribution), we selected ordinary kriging over universal kriging given the strong influence of environmental variables on the distribution of species in the study area. Data exploration of the pyrophilic percentage revealed few differences in the resulting interpolations or calculation of error terms between the two kriging methods. Trends were not removed in ordinary kriging, although anisotropy was accounted for in the final model. The number of neighboring points included in spatial calculations was set at a minimum of 2 and a maximum of 5.

To compare our product with a previously constructed, rule-based estimation of past fire regimes (Thomas-Van Gundy et al., 2007), we converted our witness-tree-based pyrophilic percentage taken from the kriged surface to fire-adaptation scores used in the rule-based estimation. A simple conversion was used by separating pyrophilic percentages into 5 evenly proportioned bins and assigning fire-adapted classes to each (0–20 pyrophilic percentage = fire-adapted class 5,...,80–100 = class 1). Fire-adaptation maps were compared by subtracting the old results from the new within 100 m grids. This calculation showed cell-by-cell departure and degrees of agreement/disagreement between the two methods.

The kriged surface described above was used to create a dataset to determine possible environmental drivers affiliated with the spatial distribution of pyrophilic and pyrophobic witness trees. To obtain a better geographic distribution across the study area (compared to the actual witness-tree points; see Fig. 2), data were derived from a 500 m point grid superimposed over the kriged pyrophilic percentage response surface. At each grid midpoint, the pyrophilic percentage and associated climate and topographic variables were extracted. We used linear regression (PROC REG, SAS, 2008) with pyrophilic percentage as the response variable and nine climate and topographic variables as predictor variables (Table 3). Predictor variables were assessed individually to describe their relationship to the pyrophilic percentage. A correlation matrix was also produced to investigate relationships among pyrophilic percentage, climatic, and topographic variables.

Relationships with environmental variables were further investigated via binary analysis. The derived pyrophilic percentage grid data were converted into two classes using a 50% breakpoint (0–50 = pyrophobic; 50.1–100 = pyrophilic), resulting in 16,844 pyrophobic points and 10,221 pyrophilic points. As before, these points were superimposed over the nine climate and topographic variables and frequency distributions for each variable were tested for differences through nonparametric one-way analysis of

Table 2
Witness trees cited in deeds dated 1752–1899 within east-central West Virginia and categorized by their relationship to fire (pyrophilic or pyrophobic). Common names are cross-walked with scientific names. A question mark after a scientific name represents uncertainty in the categorization.

Common name used in deeds	Scientific name	Relationship to fire	Vital attribute related to fire	References
Pine	*Pinus* spp.	Pyrophilic	Thick bark[a], seedbed requirements[b], needle volatility[c], early seral[d], xerophyte[e]	Abrams, 2001; Keeley, 2012
Pitch, yellow, or Virginia pine	*Pinus rigida or virginiana*	Pyrophilic	Cone serotiny, sprouting[f], needle volatility, early seral, xerophyte	FEIS, 2013; Keeley, 2012
White pine	*Pinus strobus*	Pyrophilic	Thick bark on older trees, seedbed requirements, needle volatility, early seral	FEIS, 2013; Abrams, 2001; Keeley, 2012
Red spruce, spruce, black spruce, yew pine	*Picea rubens*	Pyrophobic	Thin bark, shallow roots, late seral[d], mesophyte[e]	FEIS, 2013; White and Pickett, 1985
Yew	*Taxus canadensis, possibly Picea* (?)	Pyrophobic	Thin bark, late seral, shallow roots, shade tolerant, mesophyte	FEIS, 2013
Balsam fir, fir, balsam	*Abies balsamea*	Pyrophobic	Thin bark, late seral	FEIS, 2013
Spruce-pine	Likely *Picea rubens* or *Tsuga canadensis* (?)	Pyrophobic	Assumed to be red spruce or hemlock; thin bark, late seral, mesophyte	See citations for spruce and hemlock
Hemlock, hemlock-spruce	*Tsuga canadensis*	Pyrophobic	Thin bark, late seral, shallow roots, mesophyte	FEIS, 2013
Red cedar, cedar	*Juniperus virginiana*	Pyrophilic	Early seral, thick bark, xerophyte	FEIS, 2013
Willow	*Salix* spp.	Pyrophobic	Early seral, mesophyte, fire-discouraging leaves[g]	FEIS, 2013
Aspen, cottonwood	*Populus* spp.	Pyrophilic	Early seral, thick bark, sprouting	FEIS, 2013
Butternut, white walnut	*Juglans cinerea*	Pyrophobic	Mesophyte, fire-discouraging leaves	FEIS, 2013
Black walnut, walnut	*Juglans nigra*	Pyrophobic	Mesophyte, fire-discouraging leaves	Burns and Honkala, 1990
Hickory	*Carya* spp.	Pyrophilic	Thick bark (most species), xerophyte, tap root	FEIS, 2013
Hornbeam, ironwood, hophornbeam, Bluebeech	*Carpinus caroliniana, Ostrya virginiana*	Pyrophobic	Thin bark, late seral, shade tolerant, mesophyte, fire-encouraging leaves[g]	FEIS, 2013
Birch	*Betula* spp.	Pyrophobic	Thin bark, fire-discouraging leaves, poor sprouting, mesophyte	FEIS, 2013
Black or sweet birch	*Betula lenta*	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	Burns and Honkala, 1990
River birch	*Betula nigra*	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	FEIS, 2013
American beech	*Fagus grandifolia*	Pyrophobic	Thin bark, fire discouraging leaves, mesophyte	FEIS, 2013
Chestnut	*Castanea dentata*	Pyrophilic	Sprouting, thick bark, fire-encouraging leaves, tap root, rot resistance	Delcourt and Delcourt, 1998; Perry and Ison, 2003
Oak	*Quercus* spp.	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, xerophyte, tap root	Abrams, 1990, 2000
White oak	*Quercus alba*	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, xerophyte, tap root	FEIS, 2013
Chestnut or rock oak	*Quercus prinus*	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, xerophyte, tap root	FEIS, 2013
Northern red oak	*Quercus rubra*	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, tap root	FEIS, 2013
Scarlet, span, Spanish, or pin oak	*Quercus coccinea*	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, xerophyte, tap root	FEIS, 2013
Black oak	*Quercus velutina*	Pyrophilic	Thick bark, sprouting, fire-encouraging leaves, xerophyte, tap root	FEIS, 2013
Elm	*Ulmus* spp.	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	FEIS, 2013
Magnolia, cucumber, elkwood	*Magnolia acuminata* or *fraseri*	Pyrophobic	Thin bark, mesophyte	Burns and Honkala, 1990
Yellow-poplar, poplar, tulip tree, tulip	*Liriodendron tulipifera*	Pyrophobic	Fire-discouraging leaves, mesophyte	FEIS, 2013
Sassafras	*Sassafras albidum*	Pyrophilic	Thick bark, sprouting, early seral, xerophyte	FEIS, 2013
Sycamore	*Plantanus occidentalis*	Pyrophobic	Thin bark, mesophyte	FEIS, 2013
Apple, crab apple, plum, and peach	*Malus* spp.	Pyrophobic	Fire-discouraging leaves, mesophyte	
Serviceberry, service, sarvice	*Amelanchier* spp.	Pyrophobic	Thin bark, fire-discouraging leaves	FEIS, 2013
Black or wild cherry	*Prunus serotina*	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	FEIS, 2013
Locust	*Robinia pseudoacacia*	Pyrophilic	Thick bark, early seral, xerophyte	FEIS, 2013
Holly	*Ilex opaca*	Pyrophobic	Thin bark, mesophyte	FEIS, 2013
Maple	*Acer* spp., possibly *A. rubrum*?	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte, red maple increases in absence of fire	FEIS, 2013
Sugar or hard maple, sugar tree, sugar	*Acer saccharum*	Pyrophobic	Thin bark, fire-discouraging leaves, shade tolerant, mesophyte	FEIS, 2013
Striped maple	*Acer pensylvanicum*	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	FEIS, 2013
Buckeye	*Aesculus* spp.	Pyrophobic	Thin bark, fire-discouraging leaves, shade tolerant, mesophyte	Burns and Honkala, 1990
Basswood, yellow or white lynn, lin	*Tilia* spp.	Pyrophobic	Thin bark, shallow roots, fire-discouraging leaves, mesophyte	FEIS, 2013
Blackgum, gum, sour gum	*Nyssa sylvatica*	Pyrophilic	Thick bark	Abrams, 2007; FEIS, 2013
Dogwood	*Cornus* spp.	Pyrophilic	Susceptible to fungal disease under closed canopy	FEIS, 2013; Holzmueller et al., 2008

Table 2 (*continued*)

Common name used in deeds	Scientific name	Relationship to fire	Vital attribute related to fire	References
Sourwood	*Oxydendrum arboretum*	Pyrophilic	Sprouting, xerophyte	FEIS, 2013
Ash	*Fraxinus americana*	Pyrophobic	Fire-discouraging leaves, mesophyte	FEIS, 2013
Hawthorn, white thorn, thorn	*Crataegus* spp.	Pyrophilic	Early seral	
Hazel, witch hazel	*Corylus* (?), *Hamamelis virginiana*	Pyrophobic	Thin bark, shallow roots, mesophyte	FEIS, 2013
Indian wood, Indian bitter	*Maclura pomifera* (?)	Pyrophobic	Mesophyte	FEIS, 2013
Mulberry	*Morus* spp.	Pyrophobic	Thin bark, fire-discouraging leaves, mesophyte	

[a] Thick/thin bark on mature trees.
[b] Preference for post-fire mineral seedbeds.
[c] Leaves with volatile substances that encourage fire.
[d] Early-seral trees are shade intolerant and disturbance dependent, whereas late-seral trees are shade tolerant and disturbance independent.
[e] Xerophytes often associated with fire; mesophytes often disassociated with fire.
[f] Trees that sprout after repeated post-fire top kill/injury.
[g] Fallen leaf characteristics that encourage (thick, xeromorphic, water-repellent, and curled) or discourage surface fire (thin, flaccid, moisture-laden, adhesive and flat-lying).

variance and the Kruskal–Wallis (K–W) test (SAS, 2008) and graphically displayed.

3. Results

The spatial display of witness trees categorized by their pyrogenic relations revealed a high degree of interspersion between pyrophobic and pyrophilic species across the study area (Fig. 2). Spatial distinctions between these two groups were identified through point overlays (Fig. 2c and d). Areas where pyrophilic points were more prevalent and/or isolated from pyrophobic points included the Tygart Valley (Fig. 1, point 1, far west-central sector) and the Ridge and Valley Physiographic Province in eastern and southeastern portions of the study area (Fig 2c). Points with exclusively more pyrophobic trees were concentrated in the high mountains (Fig. 2d), essentially forming a northeast-to-southwest band across the central portion of the study area corresponding to the Appalachian Highlands (Fig. 1).

Spatial interpolations from pyrophilic percentage point data show a gradient of fire–vegetation relationships across the study area (Fig. 3). These gradients were further summarized by converting these mapped percentages to fire-adapted scores used in an older rule-based model (Fig. 4a and b). Compared to the rule-based model, the new pyrophilic percentage model resulted in (1) a more even distribution of area across fire-adaptation classes, (2) a substantial increase in the most fire-adapted class (class 1), and (3) a sizeable decrease in fire-adapted class 4 (see insert bar graphs of Fig. 4a and b).

Cell-by-cell departure calculations showed a great deal of correspondence between the two scoring methods (Table 4, Fig. 5). For instance, about 34% of the area was categorized with the same fire-adaptation score at the same location (0 difference; Table 4), whereas about 81% of the area was within one ranking category (departure of −1, 0, or 1). Most significant departures were negative (−2 to −4; Table 4), indicating the new map had more fire-adapted area than its predecessor, consistent with distribution graphs of Fig. 4a and b. Vegetation classed as more fire adapted in the new map compared to the previous one (purple in Fig. 5) were mainly concentrated in river valleys, specifically the Tygart Valley (Huttonsville), Greenbrier River (Fig. 1, point 2) and Deer Creek (Fig. 1, point 3) valleys (from Falling Spring through Marlinton to Bartow), and Seneca Creek (Fig. 1, point 4). One exception was associated with the latter (Seneca Creek/Rocks), whereby vegetation now considered more fire adapted spread into the surrounding uplands along the Allegheny Front and Fore Knobs (Fig. 5). Most positive shifts (less fire adapted) were restricted to a one-score departure and occurred within the high mountains striking across the study area. Although rare, one concentration of much reduced fire adaptation (departure scores of 2–3) occurred within the upper watershed of the North Fork of Deer Creek (southeast of Bartow) near the West Virginia–Virginia boundary.

Correlation and regression analyses of 27,065 data points from the kriged surface revealed the pyrophilic percentage to be strongly related to several environmental factors (Table 5 and Fig. 6). A significant amount of variation in the pyrophilic percentage was explained by growing season precipitation minus evapotranspiration (GSP-ET; $R^2 = 0.61$), with the percentage decreasing with increasing GSP-ET. The pyrophilic percentage also decreased with increasing mean annual precipitation (MAP; $R^2 = 0.56$), elevation (ELEV; $R^2 = 0.30$), and annual number of frost days (FROST; $R^2 = 0.19$) and increased with increasing growing degree days (GDD; $R^2 = 0.35$) and mean annual temperature (MAT; $R^2 = 0.35$) (Fig. 6). Slope, aspect, and topographic roughness had little to no explanatory value. All climate-based variables correlated with the pyrophilic percentage were correlated with elevation in a

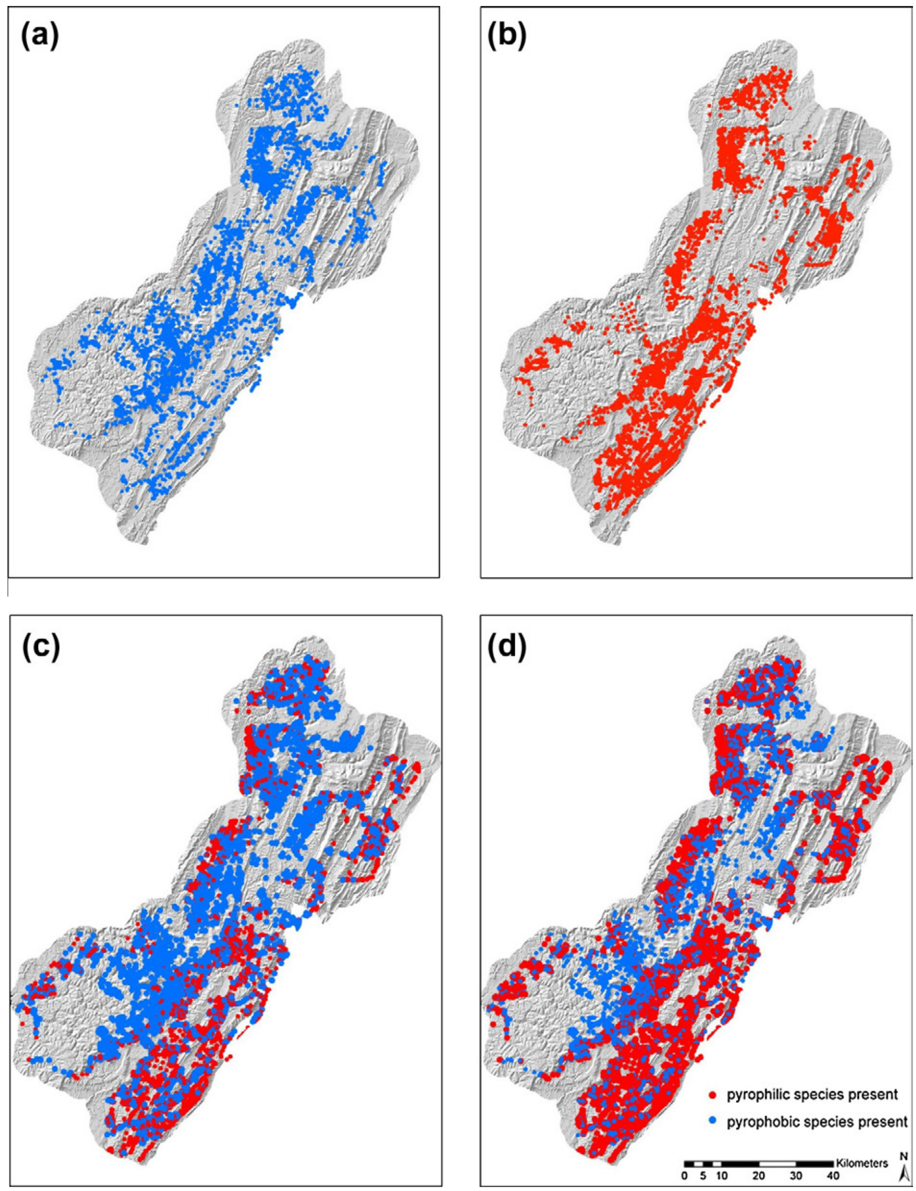

Fig. 2. Witness-tree point locations in east-central West Virginia showing (a) pyrophobic trees (blue), (b) pyrophilic trees (red), (c) pyrophobic superimposed over pyrophilic trees, and (d) pyrophilic superimposed over pyrophobic trees.

manner consistent with a climo-elevational gradient of increasing moisture (GSP-ET $r = 0.58$, MAP $r = 0.64$) and decreasing temperature (MAT $r = -0.86$, GDD $r = -0.89$, FROST $r = 0.81$) (Table 5). These topoclimatic relations support and may, in turn, largely explain the strong negative correlation found between pyrophilic percentage and elevation ($r = -0.55$).

Comparing distributional means of pyrophobic and pyrophilic points through nonparametric one-way ANOVA reinforced these findings, with pyrophilic points having significantly lower GSP-ET, MAP, FROST, and ELEV and significantly higher MAT and GDD (Fig. 7). Overall, the pyrophilic percentage corresponded to a climo-elevational gradient from warm, dry valleys (high pyrophilic percentages) to cool, wet mountaintops (low pyrophilic percentages).

4. Discussion

Understanding past disturbance regimes and emulating them through current management practices is gaining favor among land managers for ensuring ecosystem integrity and sustainability at the landscape scale (Engstrom et al., 1999; Seymour et al., 2002; Long, 2009). Restorationists are particularly attracted to the evolutionary basis of this concept, whereby past vegetation conditions may be most easily attained (and maintained) through re-establishing fundamental processes (Falk, 1990).

Witness trees not only reflect forest composition and structure at the time of survey, but also provide information on former disturbance histories based on species' ecophysiological traits. In an area where diameter was recorded for witness trees, Fralish and McCardle (2009) concluded that witness trees serve as long-term recorders of past disturbance conditions possibly spanning several hundred years before the survey date. However, the potential of witness trees as disturbance descriptors remains largely unrealized as line notes affiliated with PLS records (documenting entry and exit from a disturbed area) have normally been used to recreate past disturbance regimes rather than witness-trees themselves. The lack of line notes in metes-and-bounds surveys in our region made this shortcoming recognizable, spurring us to devise a way

Table 3
Descriptions of nine climatic and topographic variables used to analyze the pyrophilic percentage and site differences in east-central West Virginia.

Variable	Acronym	Description
Climate variables		
Mean annual temperature	MAT	The 18-year mean temperature (°C) of the average daily air temperature
Growing degree days	GDD	The 18-year mean of the annual summation of the daily average air temperatures that are >0 °C, in degree-days
Number of frost days	FROST	The 18-year mean of the number of days in an annual period when the daily minimum air temperature is ⩽0 °C
Mean annual precipitation	MAP	The 18-year mean of the total accumulated precipitation over 1 year, in cm
Growing season precipitation minus evapotranspiration	GSP-ET	Total precipitation minus potential evapotranspiration during the growing season in cm
Topographic variables		
Elevation	ELEV	Elevation in meters generated from terrain data
Slope	SLOP	Percent slope generated from terrain data.
Aspect	ASP	Aspect degrees generated from terrain data and transformed (Beers et al., 1996)
Topographic roughness index	TRI	A measure of surface variability calculated as the square root of the sum of squared differences in elevation between a cell and its eight neighboring cells (Riley et al., 1999).

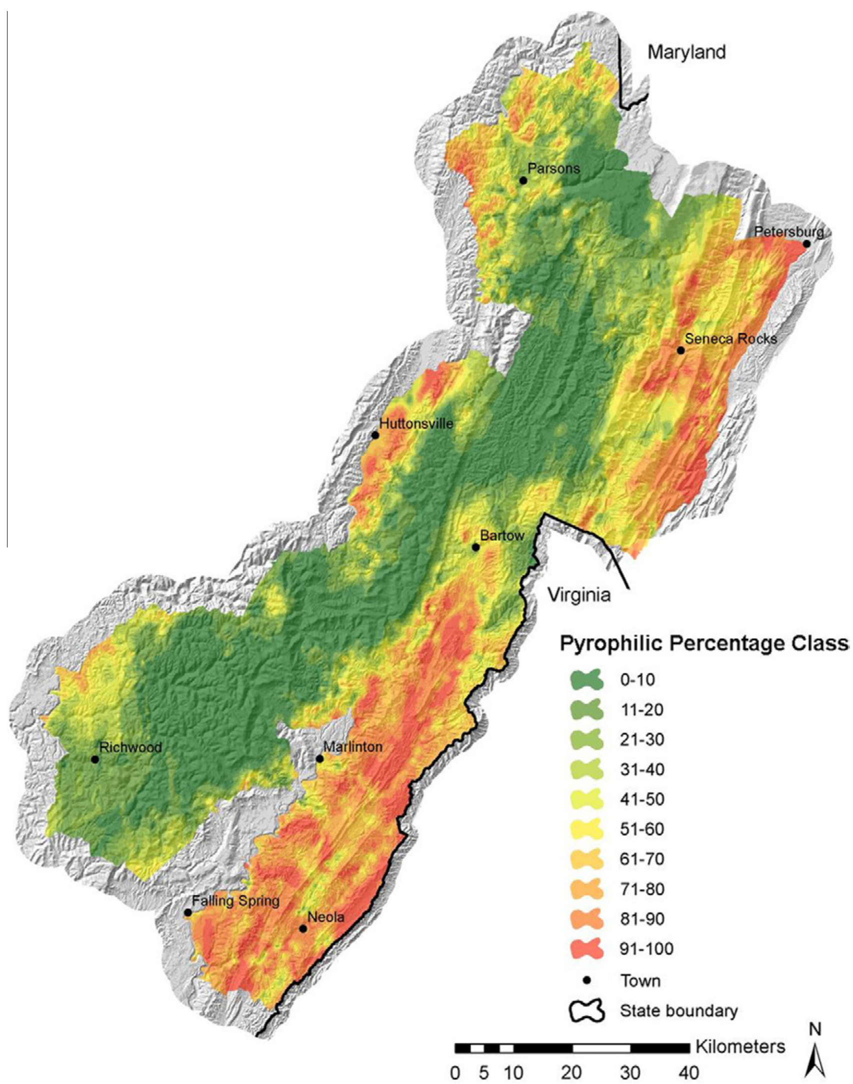

Fig. 3. A spatial depiction of the witness-tree-based pyrophilic percentage across east-central West Virginia based on ordinary kriging. Categories have been color coded to reflect a gradient from low pyrophilic percentages (witness trees predominately pyrophobic; green) to high pyrophilic percentages (trees predominately pyrophilic; red).

to use witness-tree data directly for documenting past disturbance regimes.

Through assigning fire affinities to species, we were able to directly harness witness trees as pyro-indicators and map presettlement fire regimes. Even though witness trees were simply categorized into two groups (pyrophilic and pyrophobic), spatial interpolation allowed a full gradation of fire status to be depicted from points scattered over a complex landscape. Since this approach is based directly on witness-tree data, it can be applied to both metes-and-bounds and PLS-based survey records. In our

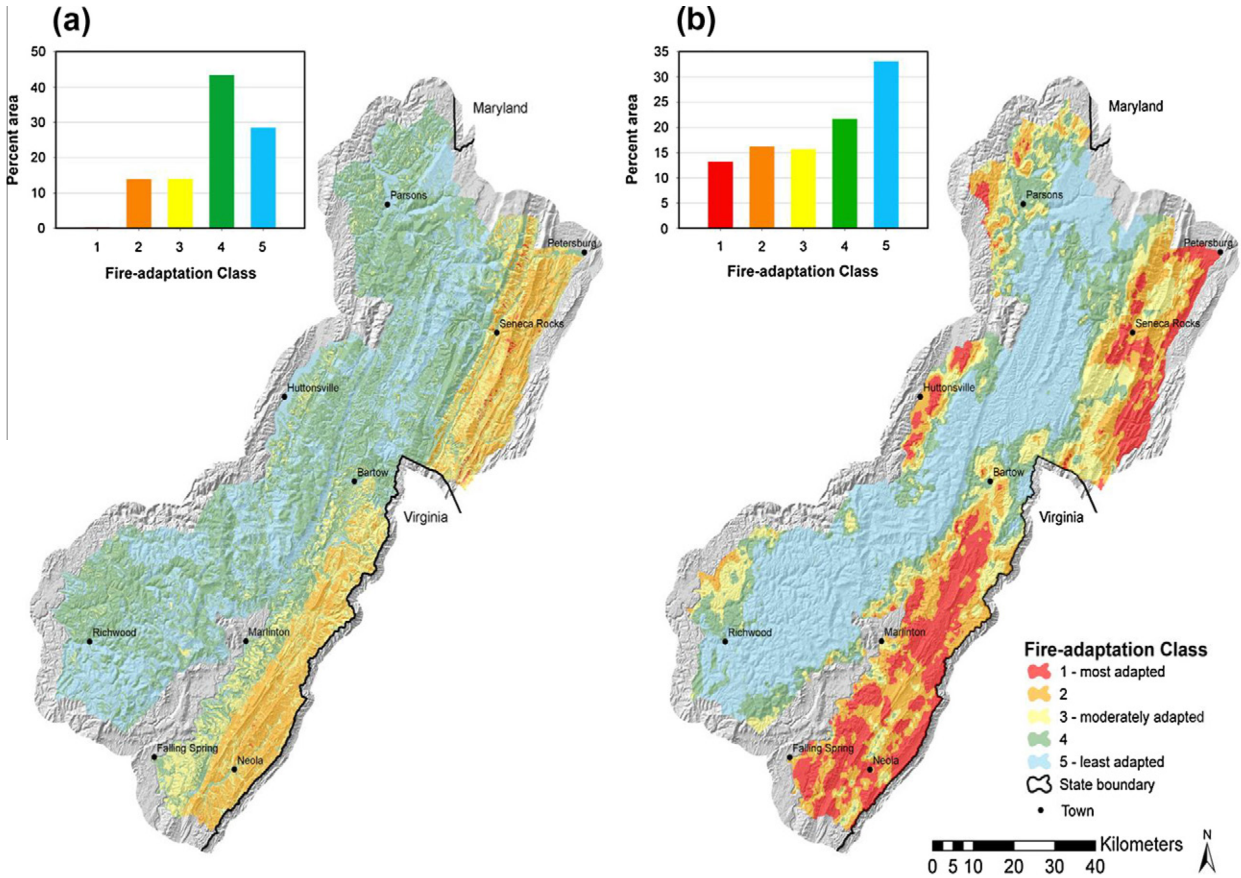

Fig. 4. A spatial depiction of fire-adapted vegetation across east-central West Virginia determined from (a) a rule-based model from Thomas-Van Gundy et al., 2007 and (b) the interpolation of a witness-tree-based pyrophilic percentage (this study).

Table 4
Agreement between the new and old models of fire-adapted rankings (rankings based on pyrophilic percent from witness trees minus rule-based model rankings).

Agreement (new–old)	Ha	% Total
−4	4891	0.7
−3	34,539	4.9
−2	88,517	12.5
−1	160,701	22.6
0	243,692	34.3
1	168,778	23.8
2	8476	1.2
3	692	0.1

particular data set, slightly more than half of the actual witness tree points had a pyrophilic percentage of either 0% or 100% since only one tree was noted in the deeds. However, when interpolated through kriging, the results were geo-spatially smoothed and appeared consistent with the ecological drivers of this diverse study area. Where direct measures of fire regimes such as fire scars in tree rings and charcoal in sediments are not available, inferring fire regimes from pyro-indicators is an appropriate alternative method.

Another limitation of inferring fire regimes through this approach is the binary nature of our categorization. Some tree species, such as eastern white pine, have traits that do not lend themselves to easy categorization of either pyrophilic or pyrophobic (e.g., thin-barked when young, yet thick-barked when old). For these species, repeated fire will remove young/small individuals and over long periods could lead to elimination of the species from a landscape. When assigning categories, we did so knowing that our study area is dominated by forests, not woodlands or grasslands where repeated disturbances discourage closed-canopy forests. We do acknowledge that additional categories capturing a broader array of fire adaptedness could add power and resolution to this approach. However, this binary method did produce maps consistent with and perhaps superior to pre-existing maps (Thomas-Van Gundy et al., 2007) based on our ecological knowledge of the study area.

Our output maps (Figs. 3 and 4b) showed fire grading from high importance at low elevations (e.g., along Tygart Valley River and Upper Greenbrier River) to low importance at high elevations. An orographic effect is clearly embedded in the dataset, with increased fire within a prominent rain shadow (i.e. Ridge and Valley Province) east of the rain-soaked Appalachian Highlands that strike diagonally across the study area. Indeed, the spatial arrangement of pyrophilic percentages essentially matches that of climate, increasing with temperature, growing season length, and water deficit and decreasing with precipitation and frost days. Since climate is inherently correlated with elevation (Nowacki and Wendt, 2010), a complex gradient of fire–vegetation–elevation–climate exists, a feature not uncommon to mountainous regions (Whittaker, 1967).

While the selected climate and topographic factors largely explained the variation existing within our pyrophilic percentage dataset, in agreement with other studies showing close climate–fire relations (Lynch and Hessl, 2010), there may be justification for exploration of other drivers. Black et al. (2006) found higher percentage of oaks and hickories (pyrophilic genera) closer to Native American village sites in northwestern Pennsylvania. They

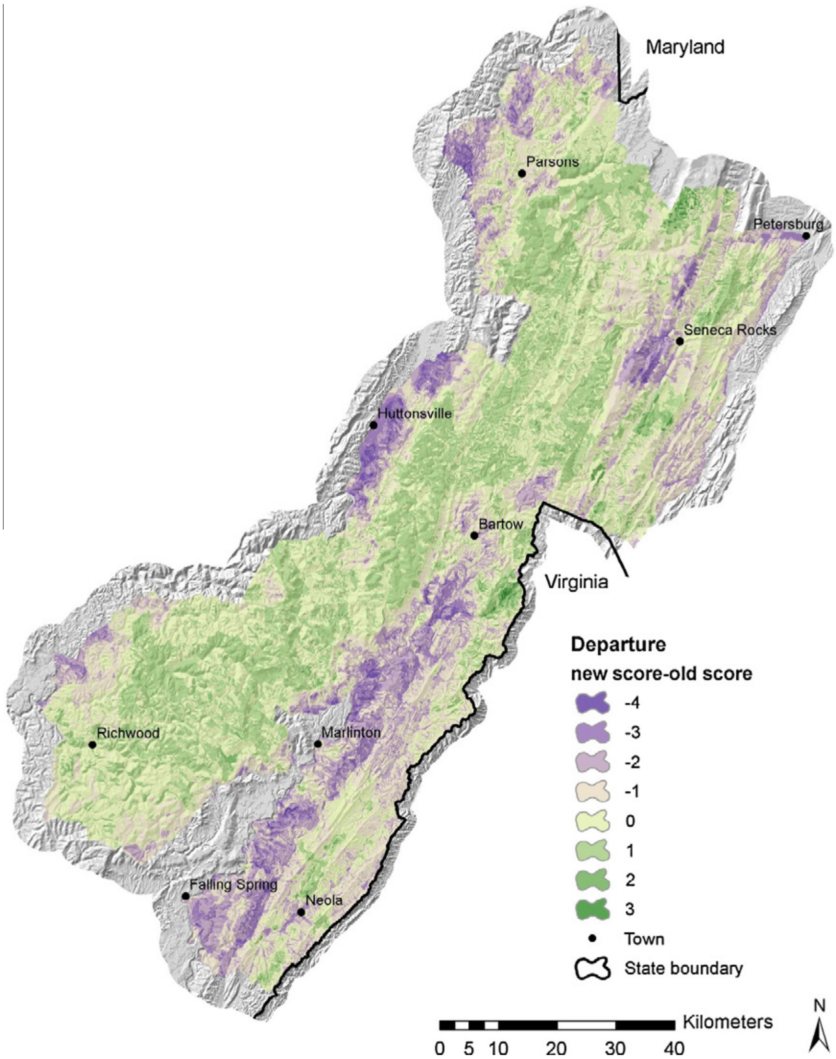

Fig. 5. Departure in fire-adapted vegetation scores between the new witness-tree-based pyrophilic percentage map and the original rule-based model (Thomas-Van Gundy et al., 2007). Negative numbers (purples) indicate more pyrophilic tendencies on the landscape according to the new map, whereas positive numbers (greens) indicate more pyrophobic tendencies on the landscape according to the new map.

Table 5
Results of correlation analysis between pyrophilic percent and climatic and topographic variables.

Variable	Pyrophilic %	GDD	FROST	MAP	MAT	GSP-ET	ASP	ELEV	SLOP	TRI
Pyrophilic %	1.00									
GDD	0.6	1.00								
FROST	−0.44	−0.95	1.00							
MAP	−0.75	−0.72	0.55	1.00						
MAT	0.59	0.96	−0.91	−0.7	1.00					
GSP-ET	−0.78	−0.62	0.47	0.88	−0.62	1.00				
ASP	−0.01	0.00	0.00	0.02	0.00	0.02	1.00			
ELEV	−0.55	−0.89	0.81	0.64	−0.86	0.58	0.03	1.00		
SLOP	0.06	0.05	−0.05	−0.08	0.06	−0.07	−0.07	−0.05	1.00	
TRI	0.1	0.11	−0.09	−0.12	0.11	−0.1	−0.07	−0.1	0.75	1.00

suggest that Native American actions converted or perpetuated the oak–hickory–chestnut forest type within an otherwise pyrophobic northern hardwood landscape. When comparing geology, landform, elevation, aspect, slope, and an index of Native American influence, the latter was found to be the most significant factor explaining the distribution of oak, hickory, and chestnut (Black et al., 2006). Closer to Native American villages, the interaction of fire, agriculture, and wood removal may have combined to result in lower white oak and greater hickory, walnut, and black locust in southeastern Pennsylvania (Black and Abrams, 2001b). Similar anthropogenic footprints may exist in our study area; especially considering Native Americans occupied the area for at least 12,000 years, with intensive utilization of river terraces and floodplains starting around 4000 years BP (Lesser, 1993). These past human influences may explain areas that appear to be anomalies, such as around Bartow, where the witness-tree-based data has resulted in more area classified as moderately fire-adapted compared to our previous mapping effort (Fig. 4).

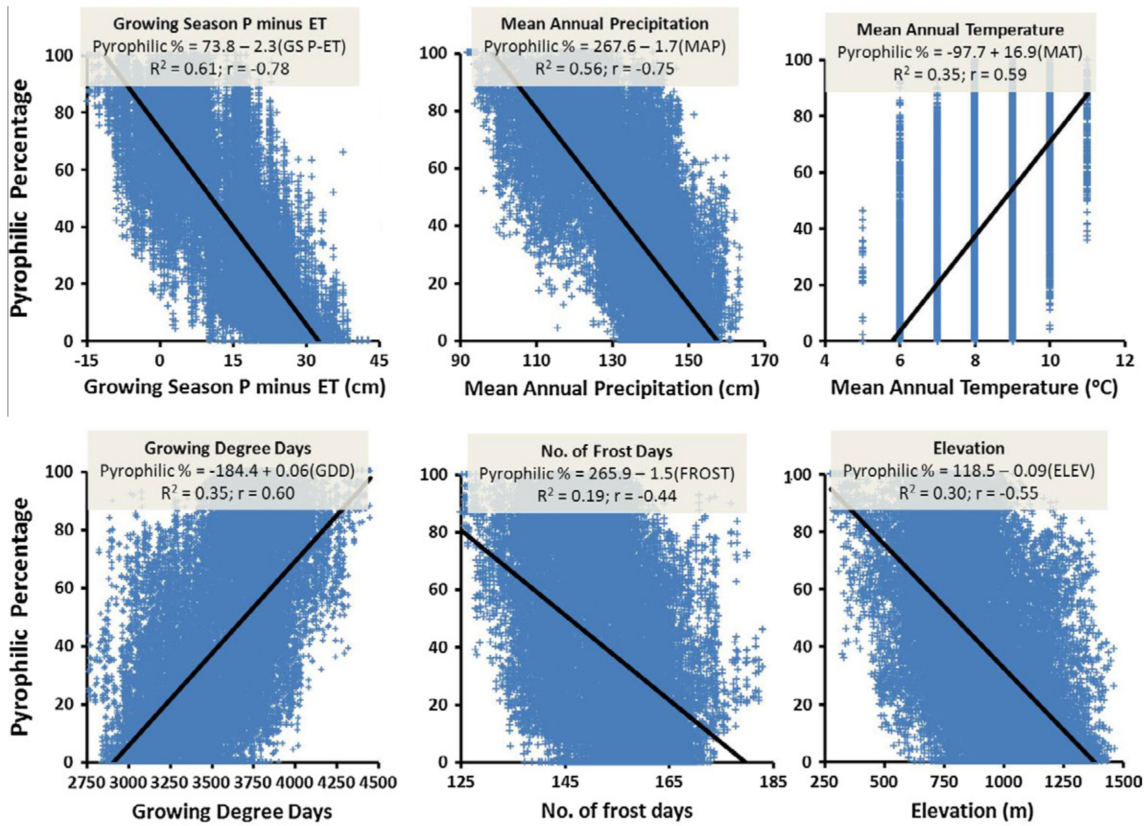

Fig. 6. Significant environmental relations between the pyrophilic percentage and 6 environmental variables based on linear regression. R^2 values are the result of regression analyses; r values are from correlation analyses.

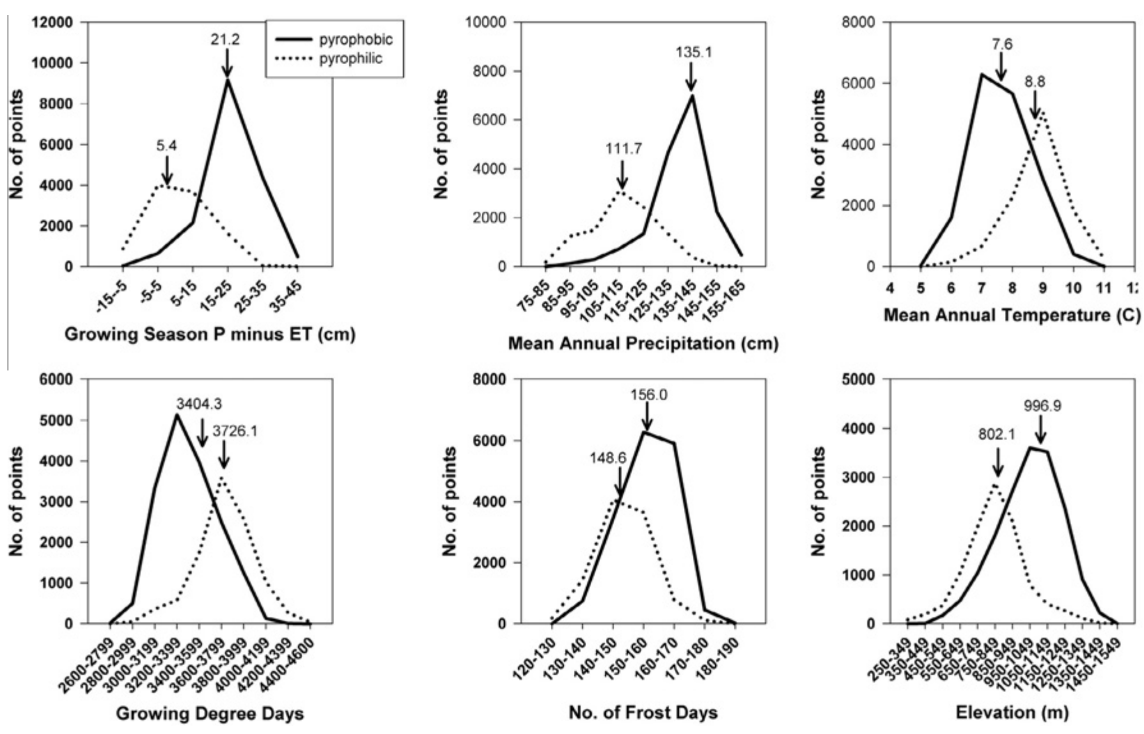

Fig. 7. Distribution and distributional mean (arrows with mean values above) comparisons of pyrophilic and pyrophobic points for 6 environmental variables. All distributions were deemed significantly different through Kruskal–Wallis nonparametric one-way analysis of variance test ($P < 0.0001$).

Although no model should be considered the absolute answer for defining presettlement fire regimes, we feel this witness-tree based effort resulted in a useful fine-scale depiction of fire–vegetation relations, better capturing landscape patterns, vegetation zonation, and spatial autocorrelations of contagious disturbances such as fire (Peterson, 2002). For instance, it resulted in larger contiguous expanses of the least adapted class (class 5) over the Appalachian Highlands characterized by very high precipitation and former ‘‘asbestos’’ red spruce-northern hardwood forests (Nowacki and Wendt, 2010). Likewise, the most fire-adapted classes converged to cover larger areas consistent with how fires would burn over drier landscapes of complex terrain resulting in oak–pine dominance (Abrams, 1992; Stambaugh and Guyette, 2008). This novel use of the witness tree record lends support and justification to the appropriate return of fire back onto formerly pyrogenic landscapes in the region (Brose et al., 2001).

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