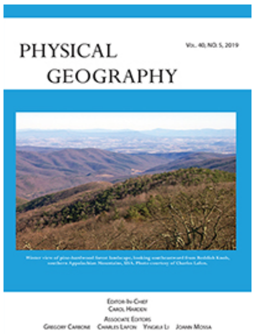

Physical Geography

ISSN: 0272-3646 (Print) 1930-0557 (Online) Journal homepage: https://www.tandfonline.com/loi/tphy20

Geographic variations in fine-scale vegetation patterns: aspect preferences of montane pine stands over Southern Appalachian landscapes

Charles W. Lafon, Alison A. Hanson & Rosemary A. Dwight

To cite this article: Charles W. Lafon, Alison A. Hanson & Rosemary A. Dwight (2019) Geographic variations in fine-scale vegetation patterns: aspect preferences of montane pine stands over Southern Appalachian landscapes, Physical Geography, 40:5, 433-460, DOI: 10.1080/02723646.2019.1576013

To link to this article: https://doi.org/10.1080/02723646.2019.1576013

Published online: 13 Feb 2019.

PHYSICAL GEOGRAPHY
2019, VOL. 40, NO. 5, 433–460
https://doi.org/10.1080/02723646.2019.1576013

ARTICLE

Geographic variations in fine-scale vegetation patterns: aspect preferences of montane pine stands over Southern Appalachian landscapes

Charles W. Lafon, Alison A. Hanson and Rosemary A. Dwight

Department of Geography, Texas A&M University, College Station, College Station, TX, USA

ABSTRACT

Landscape mosaics commonly reflect local terrain interactions with broad-scale processes. In the northern hemisphere, insolation interacts with terrain such that south-facing slopes are warmer, drier, and have sparser and more flammable vegetation than north-facing slopes. These vegetation differences are reinforced through positive feedbacks. In the southern Appalachian Mountains, USA, south-facing slopes harbor xerophytic, fire-dependent pine stands within a hardwood-forest matrix. On certain landscapes, however, pines prefer west- and northwest-facing slopes. We examine pine distribution in the southern Appalachian Mountains (Virginia through Georgia), finding that pines prefer south- and southwest-facing slopes in the southern section of this region but west-, southwest-, and northwest-facing slopes in the northern section, suggesting that broad-scale processes interact differently with terrain in the two sections. To investigate these differences, we analyze three topoclimatic factors (topographic wetness, insolation, and wind) that may influence pine distributions, and discuss other potential influences (bedrock dip, soils, and ice storms). Insolation receipt can straightforwardly explain pine distribution on southern landscapes. No single explanation accounts fully for the anomalous northern pattern, but several mechanisms (especially wind and disturbances) may contribute. We present a conceptual model of these processes and the longer-term coevolution of pine forests with microclimates, fire regimes, soils, and landforms.

ARTICLE HISTORY
Received 19 July 2018
Accepted 26 January 2019

KEYWORDS
Pinus pungens Lamb; *Pinus rigida* Mill; Table Mountain pine-pitch pine forest; topographic pattern; vegetation mosaic

Introduction

Vegetation patterns reflect the interaction of plants with two major environmental factors, stress and disturbance, of which the first limits biomass production while the second destroys existing biomass (Grime, 1977; Huston, 1994). These plant–environment interactions work through time and space to generate a patchwork of vegetation across landscapes (Forman, 1995). Such landscape mosaics arise not only through fine–scale interactions of individual plants with their environment, but through the interaction of multiple processes operating across a range of fine-to-broad scales (Peters, Bestelmeyer, & Turner, 2007). A simple but striking example is seen in the

CONTACT Charles W. Lafon clafon@geog.tamu.edu
*Present address: Halff Associates, Inc., 1201 North Bowser Rd., Richardson, TX 75081, USA

contrasting plant communities that occupy slopes of differing aspect. In the northern hemisphere, solar angle interacts with local terrain such that south-facing slopes receive more insolation than north-facing slopes, and are therefore warmer and drier. These dry conditions contribute to higher erodibility, gentler slopes, and weaker soil development as well as sparser, more flammable plant cover (Huggett, 1995; Pelletier et al., 2018; Schaetzl & Anderson, 2005).

Vegetation asymmetries between slopes are most evident where the opposing communities differ not only in species composition but also in plant physiognomy and vegetation structure, for example, between shrubland and grassland or between open woodland and dense forest (Branson & Shown, 1989; Huggett, 1995). Such vegetation contrasts provide habitat edges that influence wildlife (Ries, Fletcher, Battin, & Sisk, 2004). They can also generate feedbacks with climate, soils, and disturbance regimes that reinforce the vegetation patterns (Pelletier et al., 2018; Phillips, 2009).

In the Blue Ridge and the Ridge and Valley physiographic provinces of the Appalachian Mountains in the eastern USA, stands of xerophytic yellow pine (*Pinus*, subgenus *Diploxylon* Koehne) form patches of evergreen needleleaf forest within a deciduous broadleaf forest matrix. Our study investigates the distribution of these pine stands through the southern Appalachian region, defined here as stretching from northwestern Virginia to northern Georgia. The pine stands are generally understood to follow the typical pattern in which xerophytic plants occupy warm, dry, south- and southwest-facing slopes (Whittaker, 1956; Williams, 1998; Zobel, 1969). However, anomalous patterns are reported in some field studies that indicate pine stands are clustered primarily on west- or northwest-facing slopes that should be cooler and moister than south-facing slopes (Aldrich, Lafon, Grissino-Mayer, & DeWeese, 2014; Aldrich, Lafon, Grissino-Mayer, DeWeese, & Hoss, 2010; DeWeese, 2007; Hack & Goodlett, 1960; Zobel, 1969). These anomalous distributions are largely reported for sites in the northern (Virginia) section of the study area, while the "standard" distribution – with pines on south-facing slopes – seems characteristic in the southern section (e.g. Brose & Waldrop, 2006; Whittaker, 1956).

Most field studies have targeted only a few pine stands, and therefore it is not clear if the anomalous distribution pattern applies consistently to whole landscapes, and perhaps even to the entire northern section of the study region. If a consistent pattern emerges, it would imply that the controlling macroscale environmental factor(s) operates in the same direction over a large area. One potential factor is the prevailing wind, which would preferentially dry the windward slopes (Hack & Goodlett, 1960). Non-climatic factors might also be involved. For example, Hack and Goodlett (1960) hypothesized that bedrock structure explains the abundance of pines on northwest-facing slopes of a Virginia landscape that is situated on the southeast limb of an anticline. They proposed that as water seeps along bedding planes of southeast-dipping sedimentary strata, the northwest (scarp) slopes are dried and the southeast (dip) slopes are moistened. Hack and Goodlett showed that northwest slopes are gentler and have stonier soils than southeast slopes. These asymmetries suggested the operation of different geomorphic and pedogenic processes associated with drier conditions on the northwest slopes. The Hack and Goodlett hypothesis would provide for a consistent pine distribution over an entire region if bedrock has the same orientation throughout the region. A related possibility – but not part of the Hack and Goodlett hypothesis – is that terrain has evolved within the broad trends of Appalachian geologic structure such that xeric topographic positions, ridgetops and upper slopes, are preferentially found on west- and northwest-facing slopes in the northern section of the study region but not the southern section.

In this study, we use GIS analyses to examine pine distribution over a series of landscapes arranged from north to south through the southern Appalachian region. If it is found that pine stands show different aspect affinities between the northern and southern sections of the region, it would suggest the imprint of different macroscale environmental processes on local pine distribution. Therefore, we investigate the orientation of three topo-climatic factors – topographic wetness, insolation, and wind – that may influence pine distribution. We ask whether these factors are oriented differently on northern versus southern landscapes so as to account for regional variations in landscape-scale pine distribution.

Background: montane pine stands of the Appalachian Mountains

The montane pine stands of the Appalachian Mountains have attracted considerable attention from scientists and resource managers alike. They are part of a hardwood-pine mosaic (Figure 1) covering mountain slopes within the Blue Ridge and the Ridge and Valley physiographic provinces of the southern Appalachian Mountains. Pines are less abundant within the mesophytic forests to the west on the Appalachian Plateau, which is therefore not considered here. Pine stands are typically dominated by the Appalachian endemic Table Mountain pine (*Pinus pungens* Lamb.) and/or pitch pine (*P. rigida* Mill.) (Williams, 1998), and commonly include other yellow pine species –

Figure 1. Photograph of a southern Appalachian landscape, the Reddish Knob landscape examined in this study, showing the pine-hardwood mosaic. The evergreen pine stands, which are clearly distinct from the deciduous forest in this leaf-off photograph, form patches within the hardwood forest matrix. The pine patches occupy slopes facing the viewer. The view is from the top of Reddish Knob toward the southeast, meaning that pine stands are on the northwest-facing slopes.

Virginia pine (*P. virginiana* Mill.) or shortleaf pine (*P. echinata* Mill.). Shortleaf pine is common at low elevations in the southernmost parts of the region but not at higher elevations or northern parts of the region (e.g. Aldrich et al., 2010; Brose & Waldrop, 2006; LaForest, 2012; Simon, 2013; Simon, Collins, Kauffman, McNab, & Ulrey, 2005; Williams, 1998). The stands usually include a hardwood component, especially xerophytic oaks (*Quercus montana* Willd. and *Q. coccinea* Münchh.).

The yellow pines, which are drought-tolerant and shade-intolerant, typically inhabit upper slopes and other dry sites (Whittaker, 1956; Williams, 1998; Zobel, 1969). The pines form self-replacing populations on extremely dry rock outcrops (Barden, 1977), but most pine stands originated through disturbances and are replaced by hardwood forest without further disturbance (Williams, 1998). Fire is especially important. The dominant pines have fire adaptations including thick bark, serotinous cones, and/or post-fire sprouting (Williams, 1998). Before the era of fire exclusion, the stands appear to have been maintained under a polycyclic fire regime (Frost, 1998). First, fires of low to moderate severity burned frequently (at 2–5-year intervals; Lafon, Naito, Grissino-Mayer, Horn, & Waldrop, 2017) and benefited pine recruitment by reducing leaf litter and checking the establishment of hardwood competitors (Waldrop & Brose, 1999; Williams, 1998). Second, higher-severity fires recurred at relatively long intervals (approximately 75–100 years; Frost, 1998; Lafon et al., 2017), killing overstory trees and thereby admitting light to the understory. The fires were ignited by both people and lightning, but humans are generally thought to have been the dominant ignition source in most places (e.g. Abrams & Nowacki, 2008). Other disturbances – primarily southern pine beetle (*Dendroctonus frontalis* Zimmermann) outbreaks and ice storms (heavy freezing rain events) – also generated canopy openings and provided fuel for wildfires (Williams, 1998).

This disturbance regime, combined with the slow recovery of forest on dry, stressful sites, perpetuated pine dominance and inhibited hardwood establishment (Lafon et al., 2017). Fires that burned the pine stands would have also spread through the surrounding hardwood stands, favoring oaks and other fire-adapted hardwoods. However, fire severity was probably lower in the hardwood matrix because of less flammable hardwood litter and perhaps because of greater fuel moisture on wetter topographic positions. Moreover, plant growth rates on the moister sites would have been high enough to permit some oak sprouts and seedlings to reach a fire-resistant size between successive fires, and therefore to have enabled oaks to persist under frequent burning. Patterning of the oak-pine mosaic appears, therefore, to result from the interplay of disturbances, fuels, and plant productivity over complex terrain.

This interplay has been disrupted by fire exclusion, resulting in an ongoing decline in the extent of pine forest. The decline is exacerbated by non-fire disturbances, especially southern pine beetle outbreaks. Historically, beetle outbreaks benefited pine recruitment by opening the canopy and fueling wildfires (Williams, 1998), but fire exclusion has altered this relationship such that beetle outbreaks accelerate the successional replacement of pines by killing overstory pines without reducing the understory or leaf litter that inhibit pine establishment. Beetle-induced declines occur primarily in the southern section of the study region, where outbreaks are common (Pye, Price, Clarke, & Huggett, 2004). Outbreaks are rare in the northern section because of low winter temperatures and shorter growing seasons that limit beetle populations (Ungerer, Ayres, & Lombrardero, 1999).

Resource managers of the National Forests, National Parks, and other agencies in the southern Appalachian region are using prescribed fire to arrest declines in the abundance of montane pine stands and associated plant and animal species (e.g. National Park Service [NPS], 2010; United States Forest Service [USFS], 2014). Some of these species do not depend solely on the pine stands for habitat, but instead benefit from the landscape mosaic that comprises different community types and vegetation structure on different topographic positions (Harper, Ford, Lashley, Moorman, & Stambaugh, 2016; Rush, Klaus, Keyes, Petric, & Cooper, 2012). Therefore, this study is relevant to resource management as well as to a general understanding of Appalachian vegetation patterns. More broadly, it may suggest the possibility of other exceptions to the typical north-versus-south-slope vegetation patterning in mountainous terrain.

Research questions

Our study is guided by the following three questions:

(1) How is montane pine forest distributed with regard to aspect in the southern Appalachian region?
(2) Does this distribution vary across the southern Appalachian region?
(3) If so, are the variations related to differences in topo-climatic factors between northern and southern sections of the region?

To investigate these questions, we analyzed GIS and climatic data for 12 landscapes, each 8 × 8 km in size, distributed through the southern Appalachian region from northwestern Virginia to northern Georgia. We divided these between six northern and six southern landscapes and then compared patterns of pine forest and topo-climatic factors between the northern and southern landscapes.

Study area

The southern Appalachian Mountains

The study landscapes are distributed from northeast to southwest along the Blue Ridge and the Ridge and Valley physiographic provinces of the southern Appalachian Mountains (Figure 2). The Blue Ridge has complex mountainous terrain developed on deformed sedimentary, metamorphic, and igneous bedrock (Rodgers, 1970). The southern part of the Blue Ridge is a broad mountainous region bounded by escarpments that separate it from lower terrain on all sides, while the northern part is a narrow spine of mountains standing between areas of lower elevation. The montane pine stands occupy both northern and southern parts of the Blue Ridge and are especially abundant along its bounding escarpments (Zobel, 1969). The Ridge and Valley province consists of long, roughly parallel ridges and valleys developed on deformed sedimentary bedrock (Rodgers, 1970). The pine stands are largely restricted to parts of the Ridge and Valley – roughly north of the Virginia–Tennessee border – where high ridges form mountainous topography with suitable habitat for the stands. The southern Ridge and Valley has lower ridges and broad valleys with few montane pine stands.

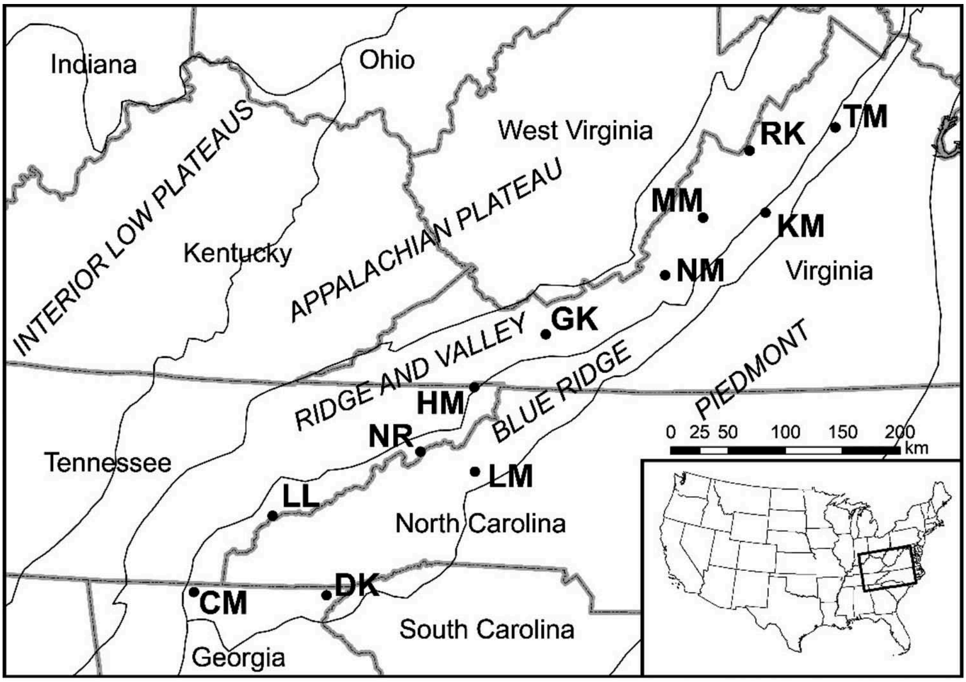

Figure 2. Map of the study area showing the location of the 12 landscapes. The two-letter abbreviations of these landscapes are defined in Table 1.

The southern Appalachian region has a humid, temperate climate with hot summers and cool winters (Bailey, 2009). Climatic means obtained for each landscape (Table 1) from PRISM (http://www.prism.oregonstate.edu/) show that for the period 1981–2010, January temperatures averaged – 0.7°C across the six northern landscapes and 1.4°C across the six southern landscapes, while July temperatures averaged 21.7°C across both northern and southern landscapes. Northern landscapes were drier than southern landscapes, with an average of 1170 mm versus 1561 mm of annual precipitation. These precipitation differences largely result from orographic effects on rainfall distribution.

The deciduous broadleaf forest that forms the general vegetation cover reflects the temperate climate of the southern Appalachian region. At the scale of local landscapes, forest types show a complex arrangement that is influenced by terrain, soils, disturbances, human manipulations, and other factors (Braun, 1950; Whittaker, 1956). In general, oak-dominated forests prevail across the mountain slopes and include several oak species mixed with hickories and other hardwood species. Mesophytic forests occupy moist coves, ravines, and north-facing slopes, while xerophytic pine-dominated stands inhabit the driest ridges and slopes.

Study sites

Of the 12 landscapes used in this study, eight were chosen to encompass sites where the first author has field research experience (Table 1), and the remaining four were distributed across other areas of the region. The landscapes were also chosen for their

Table 1. Characteristics of the 12 landscapes. An asterisk under "Field exp." Indicates the first author has field research experience on that landscape. The name of each landscape containing a field study site is the same as the name of the field site. RAWS = Remote Automated Weather Station.

Landscape	Acronym	Field exp.	RAWS (Latitude, Longitude)	Pine cover (%)	Annual ppt. (mm)	Jan temp. (°C)	Jul temp. (°C)
Northern section							
Thorofare Mtn	TM		Headquarters, VA (38°40′ N, 78°22′ W)	3.8	1391	−1.8	21.4
Reddish Knob	RK	*	Upper Tract, WV (38°49′ N, 79°17′ W)	12.4	1115	−2.1	20.4
Kelley Mtn	KM	*	Sawmill Ridge, VA (38°06′ N, 78°47′ W)	6.3	1261	−0.7	21.4
Mill Mtn	MM	*	Lime Kiln, VA (37°59′ N, 79°46′ W)	6.7	1073	−0.2	22.3
North Mtn	NM	*	Craig Valley, VA (37°31′ N, 80°05′ W)	3.1	1104	0.9	22.9
Griffith Knob	GK	*	Stony Fork, VA (37°01′ N, 81°11′ W)	2.9	1078	−0.4	21.3
Southern section							
Holston Mtn	HM	*	Nolichucky, TN (36°08′ N, 82°27′ W)	2.1	1231	0.4	21.6
Nolichucky River	NR		Nolichucky, TN (36°08′ N, 82°27′ W)	2.8	1299	1	21.4
Linville Mtn	LM	*	North Cove Pinnacle, NC (35°49′ N, 81°56′ W)	3.3	1358	0.3	20.9
Licklog	LL	*	Indian Grave, TN (35°37′ N, 83°49′ W)	2.6	1691	1.8	21.3
Double Knob	DK		Tallulah, GA (34°54′ N, 83°20′ W)	2.0	1911	2.7	22.4
Cohutta Mtn	CM		Cohutta, GA (34°55′ N, 84°39′ W)	2.3	1876	2.4	22.1

proximity to Remote Automated Weather Stations (RAWS), from which daily climate records were obtained (Table 1; https://fam.nwcg.gov/fam-web/weatherfirecd/). These records were used to investigate the strength of wind for each aspect. All the study landscapes are covered by the same vegetation dataset, which we obtained as 30-m resolution raster data from the Southeast Gap Analysis Project (SEGAP; http://www.basic.ncsu.edu/segap/). To evaluate the distribution of montane pine stands through the analyses described below, we overlaid the SEGAP layer with terrain data, which was in the form of one-arcsecond (approximately 30-m resolution) Digital Elevation Models (DEMs) obtained from the US Geological Survey (https://viewer.nationalmap.gov/basic/). The distribution of cells representing the montane pine forest (hereafter "pine cells") can be seen for a sample of four of the landscapes in Figure 3.

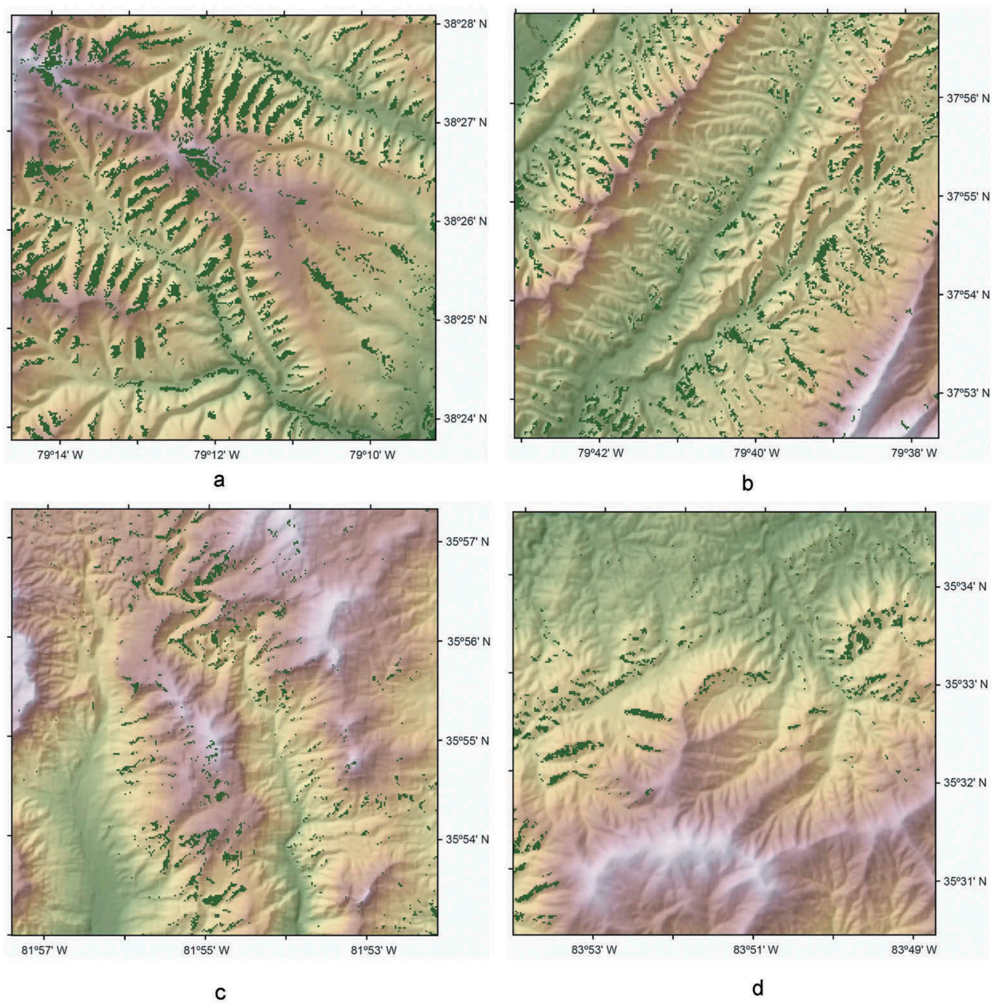

Figure 3. Shaded relief maps showing the distribution of montane pine stands (dark cells) across four of the study landscapes: (a) Reddish Knob, (b) Mill Mountain, (c) Linville Mountain, and (d) Licklog.

The pine cells were assembled by combining three of the SEGAP land cover categories. Of these categories, the predominant one is Southern Appalachian Montane Pine Forest and Woodland (NatureServe, 2007). This category represents vegetation dominated by yellow pines, particularly Table Mountain and pitch pines, but also Virginia and shortleaf pines. It also includes xerophytic oaks and a few other hardwoods. This land-cover category is the sole component of the pine cells on the six southern landscapes of our study, and it accounted for the pine forest cells on two of the northern landscapes (Thorofare Mountain and Kelley Mountain) and about half the cells on another (Griffith Knob).

Pine cells on the remaining three landscapes (Reddish Knob, Mill Mountain, and North Mountain) are composed of two other land cover types: (1) Northeastern Interior Dry-Mesic Oak Forest-Virginia/Pitch Pine Modifier and (2) Southern Ridge and Valley Dry Calcareous Forest-Pine Modifier. These are predominantly oak-hickory land cover types, modified to indicate a strong pine presence in certain cases. The names and descriptions of these two land-cover types do not seem to characterize the montane yellow pine stands as accurately as the first type, but we are confident they adequately capture the distribution of the stands.

Our confidence reflects two considerations. First, on the Griffith Knob landscape, Northeastern Interior Dry-Mesic Oak Forest-Virginia/Pitch Pine Modifier is interspersed evenly with Southern Appalachian Montane Pine Forest and Woodland. This interspersion suggests they both represent the same forest type. Second, all landscapes containing the two additional land cover categories have field study sites within them, and the pine cells mapped for this project correspond with field observations of their distribution (Aldrich et al., 2014, 2010; DeWeese, 2007). The main discrepancy with the field observations is that the GIS datasets exclude small patches of pine, an expected consequence of aggregating complex vegetation into 30 m cells. The exclusion of small patches should not affect our ability to determine which slope aspects have the greatest concentrations of pine. Only on one landscape, Reddish Knob (Figure 3(a)), does the SEGAP classification seem to include cells that do not actually represent the location of montane yellow pine stands. The cells in question appear as long strips on floodplains of the largest streams. These cells likely indicate white pine-eastern hemlock forest (Hack & Goodlett, 1960), whose inclusion could possibly blur some topographic patterns. However, the much greater abundance of proper yellow pine stands should enable us to distinguish the patterns of yellow pine.

The land-cover data indicate that montane pine stands are generally more extensive on northern than southern landscapes of the southern Appalachian study area. This variation is related to climatic variations across the region. Pine cover, as a percent of cells classified as pine (log-transformed), is negatively correlated with mean annual precipitation ($r = -0.55$, $P = 0.07$) and mean annual temperature ($r = -0.75$, $P < 0.01$). Partial correlations suggest that temperature is the more important climate factor: no relationship remains with precipitation when controlling for temperature ($r = -0.03$, $P = 0.94$), but a negative relationship remains with temperature when controlling for precipitation ($r = -0.60$, $P = 0.05$). The temperature relationship mainly involves winter temperature, not summer temperature. This distinction is manifested in the strong negative correlation of pine cover with mean January temperature ($r = -0.76$, $P < 0.01$) but not with mean July temperature ($r = -0.43$, $P = 0.17$). These relationships of pine cover with regional climate gradients seem to contradict the affinity of pines for warm, dry sites at the local scale. However, the region–scale relationships probably involve the regional gradient in southern pine beetle outbreaks, which have disproportionately affected southern landscapes. Regardless of their influence on pine abundance, beetle outbreaks are not topographically restricted (Williams, 1998) and therefore have probably had little or no influence on the topographic patterns that are the focus of this study.

The predominant soil orders across the 12 landscapes are Inceptisols and Entisols, with Ultisols and Spodosols also found on some landscapes (Table 2). Soil series generally do not vary by aspect (SoilWeb, https://casoilresource.lawr.ucdavis.edu/gmap/), but aspect preferences are depicted on certain landscapes. Notably, on the Reddish Knob landscape, the Leetonia series is mapped as narrow strips on the west- and northwest-facing slopes that are generally covered with pine forest. This soil is an Entic Haplorthod, described as an extremely stony loamy sand. We have omitted this soil from the Reddish Knob entry in Table 2 because of the small area of the landscape covered by the soil. It is more widespread on the Kelley Mountain landscape (Table 2), where it occupies broad summits and upper slopes that have some pine cover but does not form the primary habitat for pine stands. On the Holston Mountain landscape, the Ditney series, a Typic Dystrudept described as a sandy loam, is common over the landscape but shows some preference for the southwest-facing slopes covered with pine. In contrast, the Keener series (Typic

Table 2. Predominant soils on each landscape.

Landscape	Soil subgroup	Soil series
Northern section		
Thorofare Mtn	Extensive areas with no soil description	Colluvial land, Rock land
	Typic Dystrudept	Edneytown, Peaks, Porters, Tusquitee
Reddish Knob	Typic Dystrudept	Hazelton, Lehew
Kelley Mtn	Typic Dystrudept	Cataska, Hazelton
	Entic Haplorthod	Leetonia
	Typic Udorthent	Drall
Mill Mtn	Lithic Dystrudept	Weikert
	Typic Dystrudept	Berks, Dekalb
	Typic Hapludult	Lily, Oriskany
	Lithic Udorthent	Rough
North Mtn	Lithic Dystrudept	Weikert
	Typic Dystrudept	Berks, Dekalb
Griffith Knob	Lithic Dystrudept	Weikert
	Typic Dystrudept	Berks, Dekalb
	Typic Hapludult	Brushy, Lily
Southern section		
Holston Mtn	Typic Dystrudept	Cataska, Ditney
	Typic Hapludult	Cataska
Nolichucky River	Extensive areas with no soil description	Rock outcrops
	Humic Dystrudept	Chestoa
	Lithic Dystrudept	Unicoi
	Typic Dystrudept	Ditney, Soco
Linville Mtn	Lithic Dystrudept	Unicoi
	Typic Dystrudept	Ashe, Chestnut, Ditney, Soco
Licklog	Typic Dystrudept	Ditney, Soco, Stecoah
	Typic Hapludult	Junaluska, Tsali
Double Knob	No soil map coverage of this landscape	
Cohutta Mtn	Typic Dystrudept	Ashe, Porters, Tusquitee
	Cumulic Hapludept	Haywood

Source: SoilWeb (https://casoilresource.lawr.ucdavis.edu/gmap/).

Hapludult) is scattered over the Holston Mountain landscape on lower slopes and debris fans that face northwest and generally lack pine forest.

Methods

Analyses to address Question 1: How is montane pine forest distributed with regard to aspect?

To address Question 1, we calculated the aspect of the cells in the DEM for each landscape using ArcGIS (version 10.5, Esri, Inc., 1999–2016). Each landscape was divided into eight aspect classes centered on the four cardinal and the four ordinal directions. Then, for each aspect class, we used ArcGIS to extract the number of cells designated as having pine or non-pine forest. Chi-square contingency tests (Zar, 1999) were used to assess, for each landscape, whether pine frequency varied by aspect, H_0: Relative frequency of pine and non-pine forest is the same for all aspect classes. For this and other statistical tests, we report results as statistically significant where $P < 0.05$.

Analyses to address Question 2: Does this distribution vary across the southern Appalachian region?

To address Question 2, we calculated the percent of each aspect class covered with pine on each landscape. These pine percentages (hereafter "pine cover") were based on the number of pine and non-pine cells extracted for each aspect class, as described previously. We then calculated the mean pine cover by aspect for the six northern and the six southern landscapes. A Mann–Whitney test (Zar, 1999) was used to compare the pine cover between northern and southern landscapes, H_0: The percent of each aspect class covered with pine forest does not vary between the northern and southern landscapes.

Analyses to address Question 3: Are the variations in pine distribution related to differences in topo-climatic factors between northern and southern sections of the region?

To address Question 3, we examined three factors that might vary over terrain in such a way as to influence the distribution of pine stands through their effects on soil and/or fuel moisture. If these factors differ in strength among the aspect classes, they might contribute to aspect-related differences in pine cover.

The three topo-climatic factors and their characterization

The three topo-climatic factors we examined are topographic wetness, insolation, and wind. Topographic wetness was characterized through the Topographic Wetness Index (TWI; Beven & Kirkby, 1979), which is calculated using a DEM to identify topographic positions that are conducive to runoff or to accumulation of moisture. TWI typically shows low values on ridgetops and convex upper slopes and high values in valleys and concave lower slopes.

Insolation was characterized for each cell in the landscapes using the ArcGIS tool, "Area Solar Radiation," to estimate solar power density (W/m^2), which was calculated as the mean value for the equinoxes and solstices. This procedure takes into account atmospheric attenuation, shading by terrain, and the effects of latitude on sun angle and daylength. However, it does not consider shading by clouds, influences of reflected sunlight, or contributions of longwave radiation from the atmosphere.

The wind was characterized by estimating wind power density, which was calculated as W/m^2 of wind power exerted against a vertical plane oriented in the direction of each aspect class (The Royal Academy of Engineering, https://www.raeng.org.uk/publications/other/23-wind-turbine). We calculated wind power density using daily RAWS wind speed data, from which we obtained mean wind speed for the cardinal and ordinal directions. We excluded records for days with a wind speed of 0 m/s, as the wind did not have a direction on those days. We also excluded records for days when the anemometer was "frozen" at the identical compass bearing on consecutive days; such records were excluded beginning with the fourth straight day having the same compass bearing of wind. In our calculations of wind power density, we used an atmospheric density of 1.1116 kg/m^3. This is the density at 1000 m altitude, roughly the altitude of the mid-elevation pine stands, for the US standard atmosphere (U.S. Committee on Extension to the Standard Atmosphere [USCESA], 1976). We weighted wind power density for each aspect by multiplying it by the proportion of days that wind blew from each of the eight directions. Hereafter, we refer to weighted wind power density using the less precise but simpler term, "wind power."

Relationships of pine distribution to the three topo-climatic factors

These three factors could explain the aspect-related patterns of pine only if they, themselves, were associated with pine distribution. Therefore, the first step in examining their influence was to look for general relationships between pine cover and the level of each factor. To do so, we classed the values of each factor into four categories arranged from lowest to highest values. Specifically, for topographic wetness, the cells on each landscape were classed into four TWI quartiles (Zar, 1999), and ArcGIS was used to extract the number of cells in each quartile covered with pine forest. Pine cover was then calculated for each quartile. For solar power density, the cells were also classed into four insolation quartiles. ArcGIS was used to extract the number of cells in each insolation quartile covered with pine forest, and pine cover was calculated for each quartile. For wind power, the eight cardinal/ordinal directions were classed into four categories, ranging from the least windy category (consisting of the two directions with weakest winds on a landscape) to the windiest category (consisting of the two directions with strongest winds). The number of pine cells was summed across the two wind directions in each category based on the number of pine cells in each aspect class (which had been extracted previously to address Question 1). Pine cover was then calculated for each of the four wind power categories.

We averaged the pine cover for each TWI quartile across the landscapes and used a non-parametric Friedman test followed by Nemenyi multiple comparison tests (Zar, 1999) to assess whether pine cover differed among topographic positions, H_0: Pine cover is the same for all TWI quartiles. We performed the same types of comparison among insolation quartiles (H_0: Pine cover is the same for all quartiles), and among the four wind power categories (H_0: Pine cover is the same for all categories).

Variations in the three topo-climatic factors between northern and southern landscapes

To the extent that pine distribution is influenced by the topo-climatic factors, any regional differences in compass orientation of these factors may affect the aspect preference of pine stands. Therefore, we now ask whether the topo-climatic factors are oriented differently on northern than southern landscapes: are the moisture-limited sites (xeric/illuminated/windward) concentrated on different aspects of the northern landscapes than the southern ones?

To express topographic wetness in the most general way, we first combined the lowest two TWI quartiles into a single "xeric" category and the highest two TWI quartiles into a single "mesic" category. We calculated the percent of each aspect class composed of xeric cells. We then calculated the average percentage of each aspect class composed of xeric cells in the northern versus southern landscapes, and compared the percent xeric cells of each aspect class between northern and southern landscapes using a Mann–Whitney test, H_0: The percent of each aspect class composed of xeric cells does not vary between the northern and southern landscapes. We conducted the same types of comparison for insolation. The lowest two quartiles were combined into a single "shaded" category and the highest two quartiles were combined into a single "illuminated" category. A Mann–Whitney test was used to test H_0: The percent of each aspect class composed of illuminated cells does not vary between the northern and southern landscapes.

For wind, we calculated the mean wind power of each aspect class for the northern and southern landscapes. Wind power of each aspect class was compared between the northern and southern landscapes using a Mann–Whitney test, H_0: Wind power of each aspect class does not vary between the northern and southern landscapes.

Correlations of pine distribution with the topo-climatic factors by aspect

Finally, we used Pearson correlation analyses (Zar, 1999) to investigate whether the aspect preferences of pine forest are more responsive to certain topo-climatic factors in the northern section of the region than the southern, and vice versa. Specifically, for TWI, we correlated pine cover (log-transformed) of each aspect class with the percent of each aspect class covered with topographically xeric sites, H_0: Pine cover by aspect is not correlated with the percent of the aspect class composed of xeric cells. Similar analyses were conducted for insolation (H_0: Pine cover by aspect is not correlated with the percent of the aspect class composed of illuminated cells) and for wind power (H_0: Pine cover by aspect is not correlated with wind power for that aspect class).

These correlations were conducted first at the level of the northern and southern sections. Values used for each aspect were the means for that aspect class over the six landscapes in the section. Using mean values in the analyses yields ecological correlations (Johnston, 1980), which are useful for portraying general relationships for the entire section but which could exaggerate the strength of association between the variables. Therefore, to ascertain whether these general relationships apply consistently at the level of individual landscapes, we conducted identical correlation analyses for each landscape.

Results

Question 1: How is montane pine forest distributed with regard to aspect?

The relative frequency of pine cells varies among the eight aspect classes for all the landscapes (chi-square test, DF = 49, P < 0.05 for each landscape; Figure 4). Pine extent is greatest on west-, northwest-, and southwest-facing slopes of northern landscapes, and on the south- and southwest-facing slopes of southern landscapes.

Question 2: Does this distribution vary across the southern Appalachian region?

Pine forest is more extensive on northern than southern landscapes for certain aspects: west, northwest, north, northeast, and east (not statistically significant for the east; Figure 5). In contrast, south-facing slopes have greater pine cover on southern than northern landscapes, but the difference is not statistically significant (P = 0.09) at the level of P < 0.05 used here. For the remaining two aspects, southeast and southwest, pine cover is similar for the northern and southern landscapes.

Question 3: Are the variations in pine distribution related to differences in topo-climatic factors between northern and southern sections of the region?

Relationships of pine distribution to the three topo-climatic factors

In general, pine forest is associated with sites presumed to be moisture-limited. First, pine cover is greater on dry topographic positions (low TWI quartiles) than

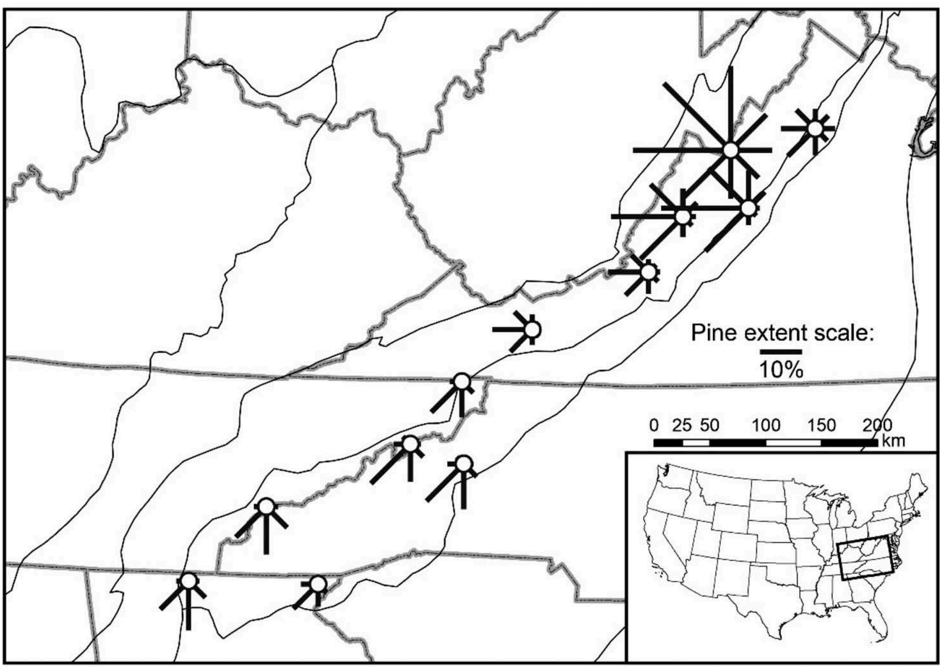

Figure 4. Pine extent for the eight aspect classes on each landscape.

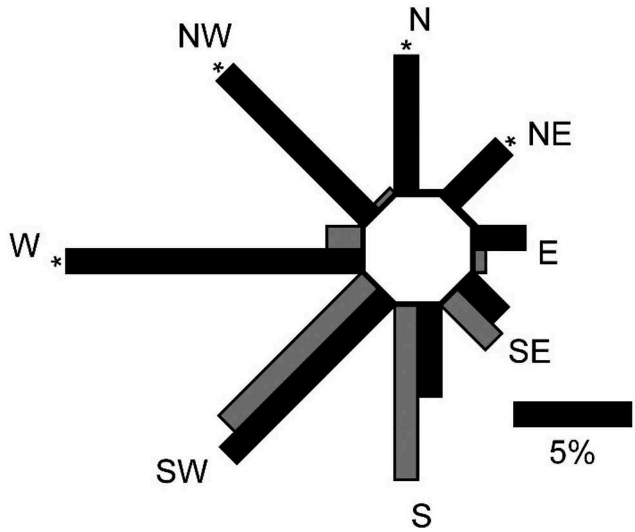

Figure 5. Mean pine cover by aspect. Black bars represent northern landscapes, and gray bars represent southern landscapes. Asterisks indicate significant differences (P < 0.05) between northern and southern landscapes, based on Mann–Whitney tests.

moist positions (high TWI quartiles; Figure 6(a)). This finding applies region-wide (all 12 landscapes combined), and also across the six landscapes in either sub-region. Second, pine cover is greater on sites with greater insolation (high insolation quartiles) than on sites with less insolation (low insolation quartiles; Figure 6 (b)). The difference is statistically significant when analyzed across all 12 landscapes or across the six southern landscapes. Third, pine cover is greater on sites with strong winds than weaker winds (Figure 6(c)). The difference is statistically significant when analyzed across all 12 landscapes or across the six northern landscapes.

Variations in the three topo-climatic factors between northern and southern landscapes

The three topo-climatic factors display relatively similar distributions by aspect in northern versus southern landscapes. With respect to topographic wetness (Figure 7(a)), the greatest disparities are for east and southeast aspects, where xeric topographic positions are approximately 1.1 times more extensive on southern than northern landscapes. These disparities do not correspond with differences in the aspect preferences of pine forest between northern and southern sections of the region. Regarding insolation, northern and southern landscapes alike receive peak illumination on south-, southeast-, and southwest-facing slopes (Figure 7(b)). The greatest insolation differences are for west and northwest aspect classes, where illuminated sites are 1.2–1.4 times more extensive on southern than northern landscapes. These disparities also do not correspond with aspect preferences of pine forest between northern and southern sections of the region. As for

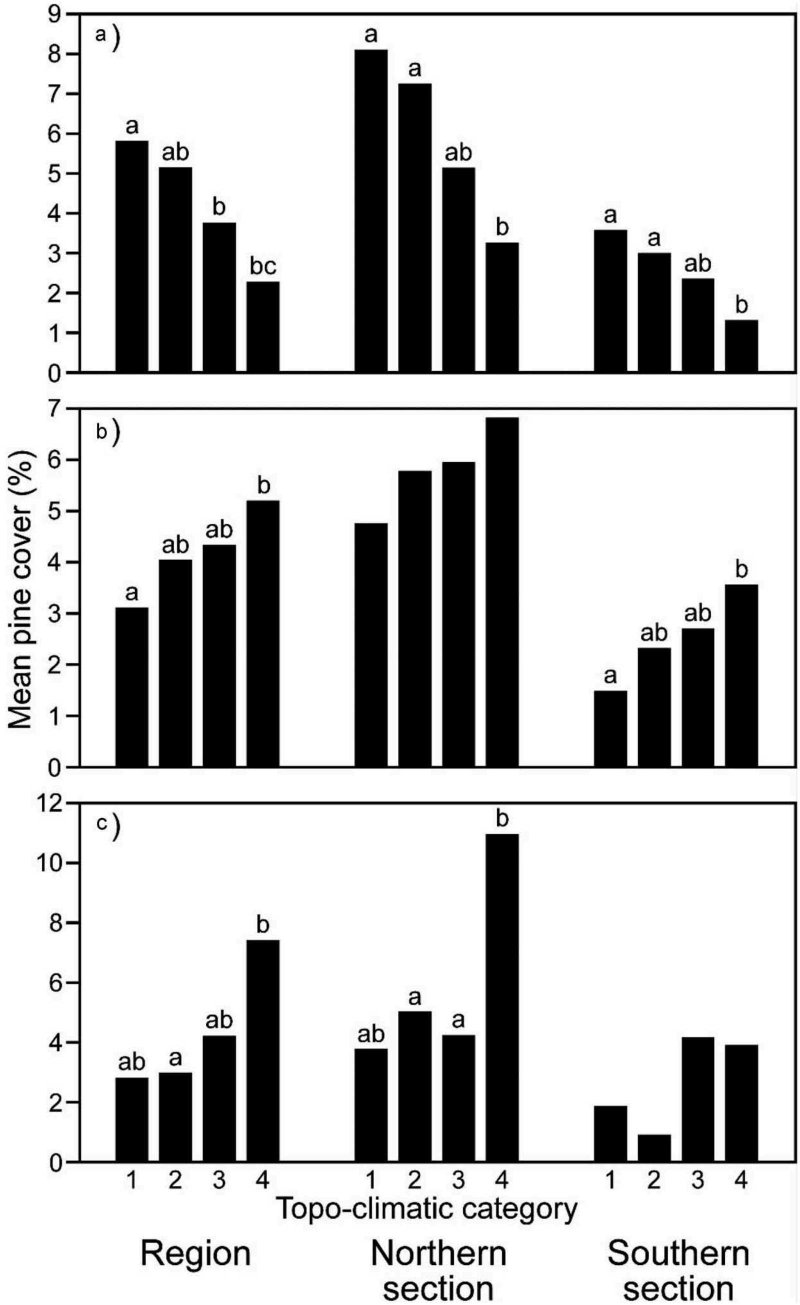

Figure 6. Mean pine cover of (a) the TWI quartiles arranged from driest to wettest (1–4), (b) the insolation quartiles arranged from least to most illuminated (1–4), and (c) the four wind power categories arranged from least to most windy (1–4). The set of bars on the left of each chart shows the means for all 12 landscapes. The middle and right sets show the means for the northern and southern landscapes, respectively. Categories labeled with different letters have significantly different pine cover (Nemenyi tests, $P < 0.05$). Unlabeled bars indicate that Nemenyi tests were not conducted because the Friedman's test did not show the categories to differ at $P < 0.05$. In the case of wind power categories, bar height does not do not correspond precisely with the order of significant differences because the non-parametric Friedman's and Nemenyi tests were conducted on ranks, not means, whereas the bar heights are based on means.

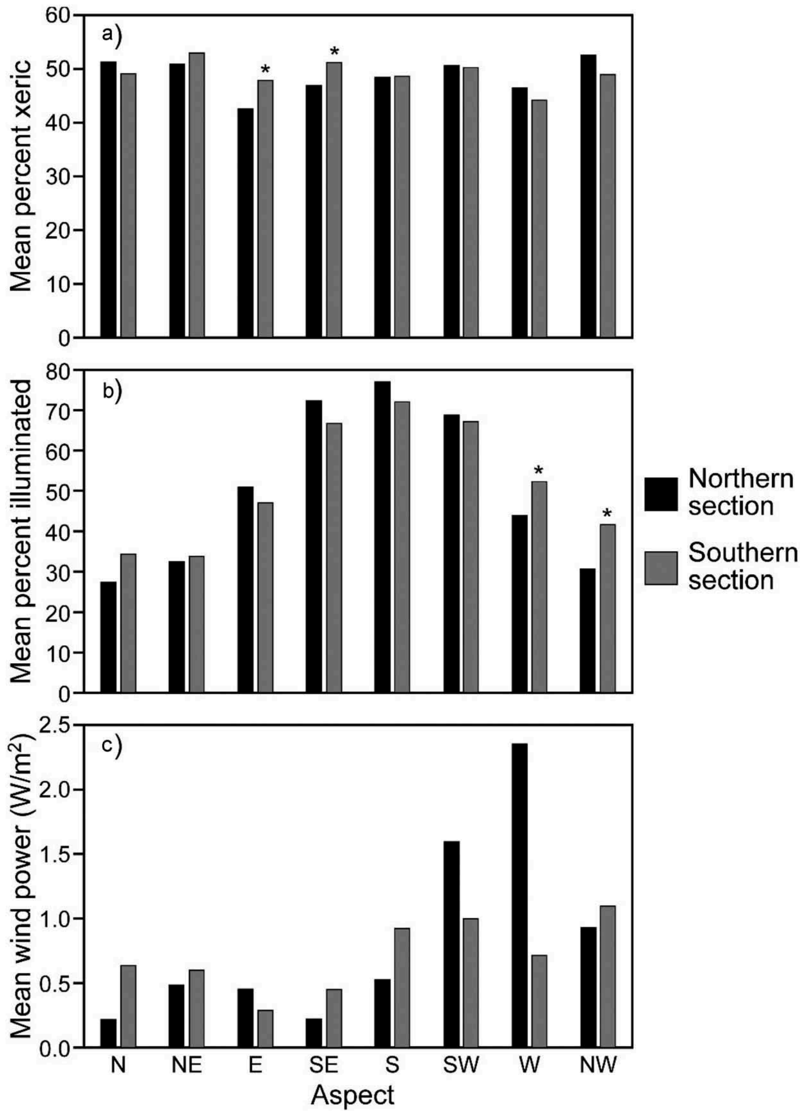

Figure 7. For each aspect class, (a) mean percent composed of xeric cells, (b) mean percent composed of illuminated cells, and (c) mean wind power. Asterisks indicate significant differences ($P < 0.05$) between northern and southern landscapes, based on Mann–Whitney tests.

mean wind power, it is generally greatest on northwest, southwest, and west aspects in both sections of the region (Figure 7(c)). It is considerably stronger for some aspects in one section or the other, but none of the differences are statistically significant because of inconsistencies among landscapes within each section. The strongest difference is for the western aspect class, where mean wind power is 3.3 times greater in northern than southern landscapes (P = 0.13). This pattern corresponds with the high abundance of pine on west-facing slopes of the northern landscapes.

In sum, pine cells are associated with topographically xeric, illuminated, and windward sites. However, these topo-climatic factors show relatively small or statistically weak variations between northern and southern landscapes in terms of their distribution among aspect classes. Moreover, the variations are not entirely consistent with the distribution of pine cells among the aspect classes.

Correlations of pine distribution with the topo-climatic factors by aspect

The next set of results investigates whether the aspect preferences of pine forest are more responsive to certain topo-climatic factors in the northern section of the region than the southern, and vice versa. These results (Table 3, Figure 8) indicate that differences in pine cover among the aspect classes are associated primarily with wind power on northern landscapes and with insolation on southern landscapes. In neither section do the variations in pine cover among aspect classes show strong or consistent associations with the distribution of topographically xeric sites.

On northern landscapes, pine cover by aspect (log-transformed) is positively related to wind power by aspect when examined at the section level via ecological correlation (r = 0.81; Table 3; Figure 8(c)). This relationship also emerges consistently, albeit more weakly, at the scale of individual landscapes (r = 0.20–0.79; Table 3).

On southern landscapes, pine cover by aspect (log-transformed) is positively associated with insolation at the section level (r = 0.98; Table 3; Figure 8(e)), meaning that pine cover is greatest on aspect classes with a large abundance of illuminated cells. This relationship is also observed consistently at the scale of individual landscapes (r = 0.80–0.98; Table 3). Additionally, pine cover shows some evidence of association with wind power on southern landscapes, but these relationships are inconsistent among the landscapes.

Discussion

This study confirms that the distribution of montane pine stands differs systematically across the southern Appalachian region. On northern landscapes, pine stands are consistently spread over several aspect classes but with peak concentrations on west-, southwest-, and northwest-facing slopes. A consistent distribution also emerges on southern landscapes: a relatively narrow clustering of pine stands on the south- and

Table 3. Correlation coefficients for the relationships of pine cover (log-transformed) with the topo-climatic variables for each aspect class. An asterisk denotes the correlation is statistically significant at $P < 0.05$.

Section/Landscape	With percent xeric	With percent illuminated	With wind power
Northern section	0.46	− 0.28	0.81*
Thorofare Mtn	0.41	0.03	0.20
Reddish Knob	0.61	− 0.61	0.64
Kelley Mtn	− 0.09	− 0.44	0.46
Mill Mtn	− 0.19	− 0.06	0.79*
North Mtn	0.35	0.20	0.61
Griffith Knob	− 0.26	0.13	0.50
Southern section	− 0.20	0.98*	0.33
Holston Mtn	− 0.43	0.81*	− 0.46
Nolichucky Riv	0.43	0.97*	− 0.46
Linville Mtn	− 0.23	0.97*	− 0.05
Licklog	− 0.74*	0.98*	0.73*
Double Knob	− 0.10	0.80*	0.42
Cohutta Mtn	− 0.24	0.98*	0.75*

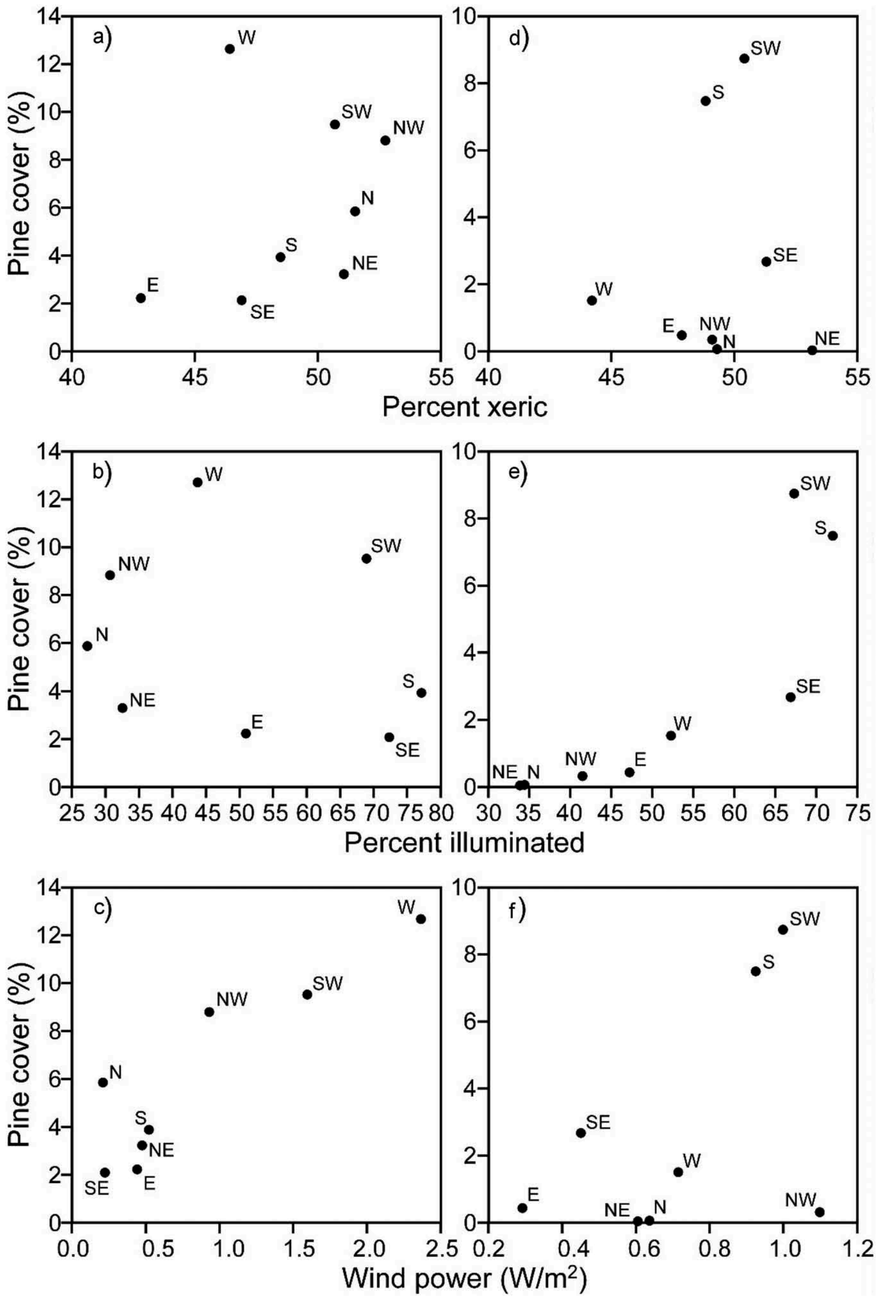

Figure 8. Scatterplots depicting the relationships between pine cover and each of the topo-climatic factors by aspect. Plots on the left (a–c) pertain to the northern section of the study region, and plots on the right (d–f) pertain to the southern section. These scatterplots are based on mean values for all landscapes in each section.

southwest-facing slopes. The southern pattern typifies xerophytic vegetation in mountains of the northern hemisphere and straightforwardly manifests the interactions between solar radiation and terrain.

On northern landscapes, insolation can only account for the abundance of pine forest on southwest slopes and its rarity on east and northeast slopes. Why pine distribution does not conform more generally to insolation patterns is not clear. One possibility is that topographic contrasts in insolation receipt are weakened or rearranged by cloud cover. However, mean annual sky cover is not much greater in the northern section of the study area than the southern section – about 60–70% versus 60% when mapped at the low spatial resolution of first-order weather stations (Environmental Data Service (EDS), 1968). High-resolution (1 km^2) estimates of insolation, which incorporate cloud cover based on satellite images, indicate the northern landscapes receive about 2–3% less radiation per year than the southern landscapes (Global Solar Atlas, http://globalsolaratlas.info/). These relatively small differences seem insufficient, in themselves, to shift pine stands away from south-facing slopes and toward the west- and northwest-facing slopes.

A more probable role of cloud cover would be to redistribute insolation within shorter time frames, especially during critical periods. For example, cloud cover differs more strongly across the Appalachian region during October and November – the peak of the fall fire season (Lafon et al., 2017) – than for the whole year (EDS, 1968). Cloudiness during those months could reduce topographic contrasts in fuel moisture and flammability on northern landscapes. For the diurnal time scale, some evidence suggests that local-scale convection arises over the Ridge and Valley during the warm season and supports early- to mid-afternoon cloudiness (Konrad, 1994). These clouds would shield south-facing slopes from the mid-day insolation peak. They would also disrupt larger convective circulations that otherwise develop later in the afternoon, as seen along the Blue Ridge (Konrad, 1994). Having disrupted late-afternoon convection, the clouds may dissipate and permit insolation onto west- and northwest-facing slopes. Whether this local-scale process could act coherently over all the landscapes of the northern section – including the two landscapes on the Blue Ridge – is a question that would need to be resolved through further research before it could be considered a probable explanation for pine distribution.

If insolation provides only a partial explanation for pine distribution on northern landscapes, do the other two topo-climatic factors we examined – topographic wetness and wind – give a further explanation? Topographically xeric sites clearly favor pine forest, but they are not oriented in a way that accounts for the aspect preference of pines. Wind is the only one of these factors that correspond to any degree with pine aspect preferences. The statistical correspondence is weak, but westerly winds may favor pine forest on west-facing slopes by drying the slopes or by driving fires up them. Fires burn more intensely when heading up windward slopes than when backing down leeward slopes (Finney, 2004). Fires burned these mountain slopes frequently in the past, before fire exclusion (Lafon et al., 2017), and if heading fires repeatedly burned west-facing slopes, they might have generated the heavy tree mortality that favored pine recruitment and thwarted hardwood establishment. Ascertaining the role of wind in driving topographic patterns of fire severity would require characterization of burn severity within recent wildfires, combined with analysis of wind power and direction during those fires. That is, wind conditions on the day of fire may be more important than mean wind power and direction for pine stand distribution.

The inability of the three factors we examined to fully explain pine distributions on northern landscapes suggests a need to consider additional explanations. One candidate is the bedrock dip hypothesis proposed by Hack and Goodlett (1960) to account for vegetation patterns in an area that encompasses the Reddish Knob landscape of our research. The landscape has largely developed on the southeast limb of an anticline, where the flow of water along southeast-dipping strata was hypothesized to dry the northwest-facing slopes of the spurs that corrugate the primary slopes of major ridges (see Figure 3(a)). For the bedrock-dip mechanism to apply on other northern landscapes would mean that the west/northwest affinity of pines results from southeast-dipping bedrock on those landscapes, too. However, bedrock does not dip uniformly to the southeast in those areas (Cooper, 1944; Gathright, 1976; Kozak, 1965; Werner, 1966; Wilkes, 2002). The Mill Mountain landscape provides a good example (Figure 3(b)). It consists of anticlinal and synclinal ridges with beds dipping southeast under some slopes and northwest under others (Kozak, 1965), but regardless of bedrock orientation, pine forest is most abundant on the west, southwest, and northwest faces of the spurs that make up the northwest side of each primary ridge. A further difficulty arises when southern landscapes are considered: pines occupy the south and southwest slopes regardless of how the sedimentary strata dip or – in areas of metamorphic rock – how bedrock foliation is oriented (Bryant & Reed, 1970; Gair & Slacke, 1982; King, Ferguson, & Hamilton, 1960; Neuman & Nelson, 1965; Peper & Moore, 1988; Rodgers, 1953).

Moreover, landform asymmetries resembling those noted by Hack and Goodlett apply on opposite sides of spurs even where bedrock dip is identical. A good example is seen on Rough Mountain, the synclinal ridge that occupies most of the northwestern side of the Mill Mountain landscape (Figure 3(b)). Bedding planes dip southeast along the entire northwestern slope of the mountain. Yet the west (pine-covered) faces of the spurs on this slope are broader and more gently sloped than the east faces of the spurs (Figure 9(a)), suggesting that west faces are drier mainly because of wind exposure or other microclimatic factors, not because they are on the scarp slope of the ridge. Similar patterns exist on the North Mountain and Griffith Knob landscapes (Figure 9(b)). Bedrock dip undoubtedly affects groundwater flow (Fan, Toran, & Schlische, 2007), but in light of these difficulties, it does not appear to be a dominant control on site moisture or pine distribution across northern or southern landscapes.

Soil type is another factor that may contribute to pine distribution because droughty or infertile soils should favor yellow pines over hardwoods (Williams, 1998). As noted above, however, soil maps indicate little preference of soil types for particular aspects. This fact implies either that aspect-related differences in soils are minimal or that the spatial resolution of the maps is too coarse to delineate small areas with distinct soils on the west-, southwest-, and northwest-facing slopes that are preferred by pines on northern landscapes. The latter possibility is suggested by the mapped soil distributions on the Reddish Knob landscape, where small polygons of the Leetonia series, a Spodosol, are mapped on pine-covered slopes that face west or northwest (SoilWeb, https://casoilresource.lawr.ucdavis.edu/gmap/). These small polygons are depicted only for the portion of the landscape within Augusta County, Virginia. In neighboring Rockingham County, Virginia, which encompasses the northeastern corner of the Reddish Knob landscape, soils are mapped at a coarser resolution that does not

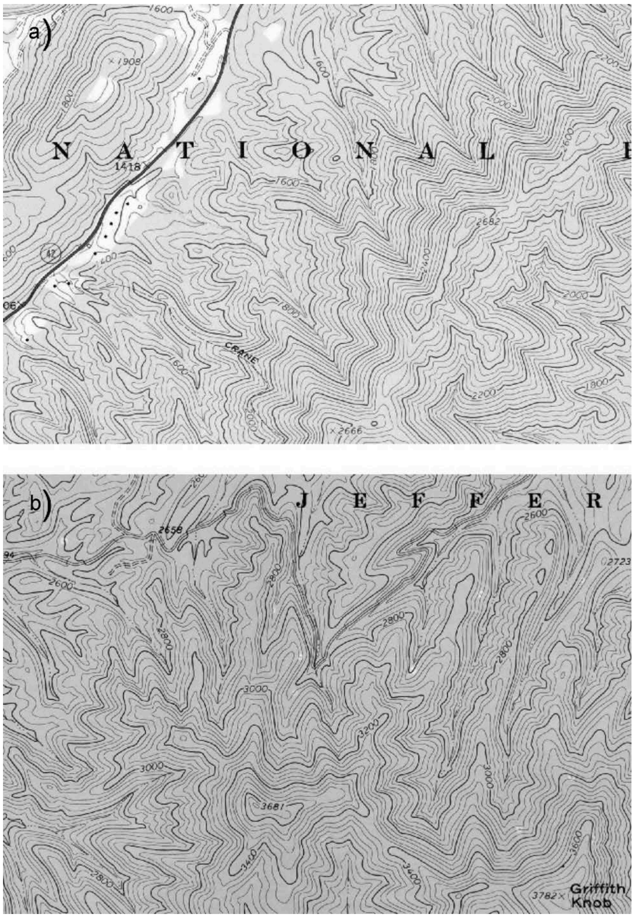

Figure 9. Topographic maps that depict portions of (a) the Mill Mountain landscape and (b) the Griffith Knob landscape. The upper panel (a) encompasses an area near the northwest corner of the Mill Mountain landscape (see Figure 3b). It is centered on the northwest slope of Rough Mountain. Asymmetry in the west versus east faces of spurs is particularly evident on the lower northwest slope of Rough Mountain, as is also the case on Griffith Knob, seen in panel B. These maps are portions of the US Geological Survey 7.5-min topographic quadrangles, published at 1:24,000 scale and reduced here to 1:40,000 scale. Panel A is from the Nimrod Hall, Virginia quadrangle (1969), and panel B is from the Big Bend, Virginia quadrangle (1968).

accommodate small polygons of Leetonia. Given that these small patches are barely mapped for the Reddish Knob landscape, which has the greatest pine cover of all 12 landscapes in our study, it is unsurprising that distinct soils are not mapped for pine-covered slopes on other landscapes, even if they exist. Alternatively, these distinct soils may truly be absent from other landscapes, in which case their presence on the Reddish Knob landscape may have contributed to the abundance of yellow pine there.

One mechanism that has undoubtedly shaped pine distribution is non-fire disturbance that kills overstory pines but, unlike fires, causes little damage to understory vegetation. Southern pine beetles are one such agent of disturbance, but as noted above, they are mostly restricted to the southern section of the study region and do not show strong aspect preferences. In the northern section, ice storms are common, and they exhibit pronounced topographic patterning. Ice storm frequency declines from northeast to southwest within the study area, a consequence of cold-air damming and trapping events along the eastern slopes of the Blue Ridge and in the Virginia portion of the Ridge and Valley (Lafon, 2016). As cold, lower-tropospheric air encounters mountainous terrain, the synoptic-scale pressure gradient becomes oriented such that winds blow from the south, southeast, east, or sometimes northeast. During an ice storm, therefore, the wind blows opposite the normal direction of the prevailing wind – windward aspects during an ice storm are the south, southeast, east, or northeast slopes. These windward slopes apparently receive greater ice accumulations than leeward slopes because of orographic effects on rainfall and/or enhanced cooling of raindrops on windward slopes (Lafon, Graybeal, & Orvis, 1999), and therefore sustain heavier forest damage. Within damaged patches, tree mortality varies among species (Lafon, 2016), with yellow pines sustaining particularly high mortality while oaks and some other species are less affected. Repeated disturbance by ice storms probably contributed to the low cover of pine forest on south-, southeast-, east-, and northeast-facing slopes.

Conclusions

The patterning of pine forest on landscapes within the southern section of the southern Appalachian Mountains can largely be explained by variations in insolation receipt by aspect. To the extent that wind, fire, or other factors are involved, they are overwhelmed by solar radiation, or their influence aligns with it. In contrast, pine distribution on northern landscapes may involve the interplay of multiple processes operating in different directions such that only a partial explanation – high pine cover on southwest slopes and low cover on east and northeast slopes – can be offered by the standard insolation model. Drying winds and severe wind-driven fires seem, provisionally, a good explanation for pines on west-, northwest-, and north-facing slopes, while ice storms help explain the rarity of pines on the south- and southeast-facing slopes. These and other potential explanations involve processes that operate at different spatial and temporal scales to form consistent landscape-scale vegetation patterns over large sections of the southern Appalachian region. The dominant processes appear to change in the vicinity of the southern Virginia border such that landscape patterning of pine forest shifts abruptly between northern and southern landscapes.

Added to the direct ecological interactions manifest through these processes would be the historical perpetuation and sharpening of vegetation patterns through positive feedbacks. For example, the development of xerophytic vegetation on dry sites can help perpetuate xeric conditions through an open stand structure that admits drying wind and sun to the forest floor (Pelletier et al., 2018). Additionally, pines not only thrive on dry, fire-prone sites, they also encourage severe fires through their flammability (Lafon et al., 2017).

The persistence of landscape configurations under positive feedbacks would mean that present vegetation patterns are partly inherited from past ecological interactions. If those interactions differed from present ones, they could help account for the weak relationships we observed between pine cover and topo-climatic factors on northern landscapes. Indeed, the geomorphic form of west-facing slopes suggests they evolved under a long history of xeric conditions (Hack & Goodlett, 1960), which probably existed before the Holocene (cf. Pelletier et al., 2018). Those conditions may have been initiated during the Pleistocene by interactions that no longer occur; but once established, xeric microclimates endured. They have coevolved with landforms, soils, vegetation, and disturbance regimes to perpetuate landscape patterns (e.g. Phillips, 2009).

Most likely, the distribution of Appalachian pine stands reflects both historical and present ecological interactions whose effects cannot be fully separated, as summarized in Figure 10. The ecological relationships emphasized in this paper are indicated in the center column of the diagram. They include topo-climatic effects on the levels of stress and disturbance that favor pine forest on certain aspects (solid downward arrows). Also, acting at relatively short time scales are positive feedbacks, e.g., on fire severity, that result from the presence of pine forest (solid upward arrows).

Historical interactions that emerge over centuries to millennia are indicated on the left and right sides of the diagram. Pine traits (left side) reflect evolutionary tradeoffs entailed in long-term habitation of stressful, fire-prone sites (Grime, 1977). For the pine species to have coevolved with the particular sites they now occupy would require their presence over many generations. *Diploxylon* pines have inhabited the southern Appalachian Mountains and surrounding regions since the Pleistocene, according to fossil pollen and needles (e.g. Ballard, Horn, & Li, 2017; Craig, 1969). The Pleistocene pine fossils have commonly been interpreted as evidencing the boreal species, jack pine

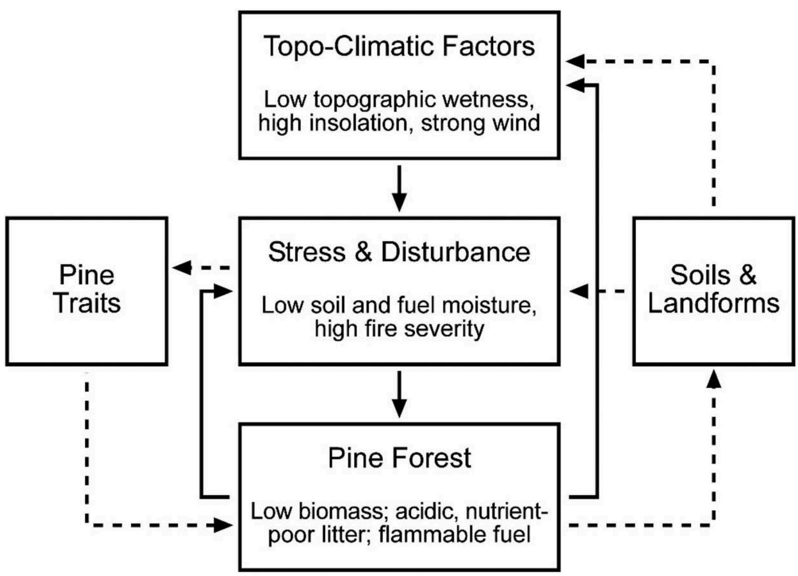

Figure 10. Conceptual model of ecological and historical interactions that favor the development and persistence of yellow pine patches on southern Appalachian landscapes. The central column of the diagram pertains to ecological interactions that are linked closely to the topo-climatic factors considered in the present study. Solid, downward-pointing arrows indicate positive influences on pine forest, and solid upward-pointing arrows indicate positive feedbacks that result from the presence of pine forest. The left and right rectangles and the dashed arrows reflect historical interactions that contribute to the coevolution of microclimates, landforms, soils, vegetation, and disturbance regimes that perpetuate pine forest.

(*Pinus banksiana* Lamb.), but uncertainties in distinguishing among the *Diploxylon* species mean that other yellow pines (e.g. Table Mountain pine) might have been present (Loehle & Iltis, 1997).

The exact species mix notwithstanding, nutrient cycling is affected by pine litter quality and favors the development of infertile, acidic soils (e.g. Spodosols; right side, bottom dashed arrow; Scholes & Nowicki, 1998). Further, low biomass in xerophytic pine stands provides only modest protection against erosion, resulting in broad, relatively gentle slopes with shallow soils (Figure 9; Pelletier et al., 2018). These soils reinforce the stressful environment that favors pine dominance (middle dashed arrow). Moreover, as the slopes evolve on xeric sites, they would appear to broaden and orient toward the prevalent topo-climatic factors acting on the landscape (e.g. Figure 9), such that pine forest indirectly influences its exposure to these factors through landform evolution (top dashed arrow). Consequently, paleoclimatic conditions may be implicated in the present arrangement of terrain and vegetation. For example, if westerly/northwesterly winds prevailed in the northern section of the study area during the Pleistocene, and southwesterly winds in the southern section, they could help account for the differences in pine distribution observed today. Appalachian paleowinds are little known, but subcontinental-scale paleo-wind reconstructions would permit such an interpretation, among others (Bromwich, Toracinta, Oglesby, Fastook, & Hughes, 2005).

The Appalachian pine stands are part of a larger mosaic of montane vegetation that has emerged through ecological, climatic, and geomorphic interactions and feedbacks that operate over multiple scales of time and space. These mechanisms expose different parts of a landscape to contrasting stresses and disturbance regimes, thereby yielding the hetero-geneous patchwork of vegetation observed in mountainous landscapes. Ongoing changes in stress (e.g. through climate change or forest stand crowding) and disturbance regimes (e.g. fire exclusion) are altering vegetation patterns in the southern Appalachian Mountains and other regions. Some of the changes can be managed to conserve vegetation patterns. Prescribed burning, when implemented over large areas (Harper et al., 2016), offers a particularly effective way to perpetuate landscape mosaics through the interaction of fire with existing heterogeneity in microclimate, terrain, and vegetation.

Acknowledgments

This paper benefited from discussions with Dave Cairns, Steve Croy, Will Flatley, Henri Grissino-Mayer, Adam Naito, and Ben Wu. We thank two anonymous reviewers for their insightful comments that helped us improve the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Charles W. Lafon http://orcid.org/0000-0001-7997-6935
Rosemary A. Dwight http://orcid.org/0000-0003-0392-2695

References

Abrams, M. D., & Nowacki, G. J. (2008). Native Americans as active and passive promoters of mast and fruit trees in the eastern USA. *The Holocene*, *18*(7), 1123–1137.

Aldrich, S. R., Lafon, C. W., Grissino-Mayer, H. D., & DeWeese, G. G. (2014). Fire history and its relations with land use and climate over three centuries in the central Appalachian Mountains, USA. *Journal of Biogeography*, *41*(11), 2093–2104.

Aldrich, S. R., Lafon, C. W., Grissino-Mayer, H. D., DeWeese, G. G., & Hoss, J. A. (2010). Three centuries of fire in montane pine-oak stands on a temperate forest landscape. *Applied Vegetation Science*, *13*(1), 36–46.

Bailey, R. G. (2009). *Ecosystem geography: From ecoregions to sites* (2nd ed.). New York, NY: Springer.

Ballard, J. P., Horn, S. P., & Li, Z. H. (2017). A 23,000-year microscopic charcoal record from Anderson Pond, Tennessee, USA. *Palynology*, *41*(2), 216–229.

Barden, L. S. (1977). Self-maintaining populations of pinus-pungens lam in Southern Appalachian Mountains. *Castanea*, *42*(4), 316–323.

Beven, K. J., & Kirkby, M. J. (1979). A physically based, variable contributing area model of basin hydrology. *Hydrological Sciences Journal*, *24*(1), 43–69.

Branson, F. A., & Shown, L. M. (1989). *Contrasts of vegetation, soils, microclimates, and geomorphic processes between North- and South-Facing slopes on Green Mountain near Denver, Colorado*. Water-Resources Investigations Report 89-4094. Denver, CO: US Geological Survey.

Braun, E. L. (1950). *Deciduous forests of Eastern North America*. Philadelphia, PA: Blakiston.

Bromwich, D. H., Toracinta, E. R., Oglesby, R. J., Fastook, J. L., & Hughes, T. J. (2005). LGM summer climate on the southern margin of the Laurentide ice sheet: Wet or dry? *Journal of Climate*, *18*(16), 3317–3338.

Brose, P. H., & Waldrop, T. A. (2006). Fire and the origin of Table Mountain pine - pitch pine communities in the southern Appalachian Mountains, USA. *Canadian Journal of Forest Research*, *36*(3), 710–718.

Bryant, B., & Reed, J. C., Jr. (1970). Geology of the grandfather mountain window and Vicinity, North Carolina and Tennessee. *Geological survey professional paper 615*. Washington, DC: US Government Printing Office.

Cooper, B. N. (1944). *Geology and mineral resources of the Burkes Garden Quadrangle, Virginia* (Bulletin 60). Charlottesville, VA: Virginia Geological Survey.

Craig, A. J. (1969). Vegetational history of the Shenandoah Valley, Virginia. *Geological society of america special paper 123* (pp. 283–296).

DeWeese, G. G. (2007). *Past fire regimes of Table Mountain pine (Pinus pungens L.) stands in the central Appalachian* Mountains, *Virginia, U.S.A* (Ph.D.). University of Tennessee, Knoxville, TN.

EDS. (1968). *Climatic Atlas of the United States*. Washington, DC: US Government Printing Office.

Esri. (1999–2016). ArcGIS (Version 10.5).

Fan, Y., Toran, L., & Schlische, R. W. (2007). Groundwater flow and groundwater-stream interaction in fractured and dipping sedimentary rocks: Insights from numerical models. *Water Resources Research*, *43*(1). doi:10.1029/2006wr004864

Finney, M. A. (2004). FARSITE: Fire Area Simulator-Model Development and Evaluation. *Research paper RMRS-RP-4 revised*. Missoula, MT: Rocky Mountain Research Station.

Forman, R. T. T. (1995). *Land Mosaics: The ecology of landscapes and regions*. Cambridge, UK: Cambridge Univeristy Press.

Frost, C. C. (1998). Presettlement fire frequency regimes of the United States: A first approximation. *Tall Timbers Fire Ecology Conference*. (Vol. *20*, pp. 70–81).

Gair, J. E., & Slacke, J. F. (1982). *Geologic maps of the cohutta wilderness and the hemp top roadless area, Northern Georgia and Southeastern Tennessee* (Map MF-1415-A). Reston, VA: US Geological Survey.

Gathright, T. M., Jr. (1976). *Geology of the Shenandoah National Park, Virginia* (Bulletin 86). Charlottesville, VA: Virginia Division of Mineral Resources.

Grime, J. P. (1977). Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, *111*(982), 1169–1194.
Hack, J. T., & Goodlett, J. C. (1960). Geomorphology and forest ecology of a Mountain Region in the central Appalachians. *Geological survey professional paper 347*. Washington, DC: United States Government Printing Office.
Harper, C. A., Ford, W. M., Lashley, M. A., Moorman, C. E., & Stambaugh, M. C. (2016). Fire effects on wildlife in the central hardwoods and Appalachian Regions, USA. *Fire Ecology*, *12* (2), 127–159.
Huggett, R. J. (1995). *Geoecology*. London, UK: Routledge.
Huston, M. A. (1994). *Biological diversity: The coexistence of species on changing landscapes*. Cambridge, UK: Cambridge University Press.
Johnston, R. J. (1980). *Multivariate statistical analysis in geography*. New York, NY: Longman Scientific & Technical.
King, P. B., Ferguson, H. W., & Hamilton, W. (1960). Geology of Northeasternmost Tennessee. *Geological survey professional paper 311*. Washington, DC: US Government Printing Office.
Konrad, C. E. (1994). Moisture trajectories associated with heavy rainfall in the Appalachian Region of the United-States. *Physical Geography*, *15*(3), 227–248.
Kozak, S. J. (1965). *Geology of the Millboro Quadrangle, Virginia* (Report of Investigations 8). Charlottesville, VA: Virginia Divsion of Mineral Resources.
Lafon, C. W. (2016). Ice storms in central hardwood forests: The disturbance regime, spatial patterns, and vegetation influences. In C. H. Greenberg & B. S. Collins (Eds.), *Natural disturbances and historic range of variation: type, frequency, severity, and post-disturbance structure in Central Hardwood Forests USA* (pp. 147–166). Cham, Switzerland: Springer.
Lafon, C. W., Graybeal, D. Y., & Orvis, K. H. (1999). Patterns of ice accumulation and forest disturbance during two ice storms in southwestern Virginia. *Physical Geography*, *20*(2), 97–115.
Lafon, C. W., Naito, A. T., Grissino-Mayer, H. D., Horn, S. P., & Waldrop, T. A. (2017). *Fire history of the appalachian region: A review and synthesis* (General Technical Report SRS-219). Asheville, NC: Southern Research Station.
LaForest, L. B. (2012). *Fire regimes of lower-elevation forest in Great Smoky Mountains National Park, Tennessee, U.S.A* (Ph.D.). University of Tennessee, Knoxville, TN.
Loehle, C., & Iltis, H. (1997). *The pleistocene biogeography of Eastern North America: A nonmigration scenario for deciduous forest* (ANL/ER/PP-90468). Argonne, IL.
NatureServe. (2007). *International ecological classification standard: Terrestrial ecological classifications*. Arlington, VA: Author.
Neuman, R. B., & Nelson, W. H. (1965). Geology of the Great Smoky Mountains, Tennessee. *Geological survey professional paper 349-D*. Washington, DC: US Government Printing Office.
NPS. (2010). *Great Smoky Mountains National Park Fire Management Plan*. Gatlinburg, TN: National Park Service.
Pelletier, J. D., Barron-Gafford, G. A., Gutierrez-Jurado, H., Hinckley, E. L. S., Istanbulluoglu, E., McGuire, L. A., Tucker, G. E. (2018). Which way do you lean? Using slope aspect variations to understand critical zone processes and feedbacks. *Earth Surface Processes and Landforms*, *43* (5), 1133–1154.
Peper, J. D., & Moore, W. J. (1988). *Geologic map of the rabun bald roadless area, Rabun County, Georgia* (Map MF-1946-A). Reston, VA: US Geological Survey.
Peters, D. P. C., Bestelmeyer, B. T., & Turner, M. G. (2007). Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. *Ecosystems*, *10* (5), 790–796.
Phillips, J. D. (2009). Soils as extended composite phenotypes. *Geoderma*, *149*(1–2), 143–151.
Pye, J. M., Price, T. S., Clarke, S. R., & Huggett, R. J., Jr. (2004). A history of southern pine beetle outbreaks in the southeastern united states through 2004. Retrieved from https://www.srs.fs.usda.gov/econ/data/spb-withheld/

Ries, L., Fletcher, R. J., Battin, J., & Sisk, T. D. (2004). Ecological responses to habitat edges: Mechanisms, models, and variability explained. *Annual Review of Ecology Evolution and Systematics*, *35*, 491–522.

Rodgers, J. (1953). *Geologic map of east tennessee with explanatory text* (Bulletin 58). Nashville, TN: Tennessee Division of Geology.

Rodgers, J. (1970). *The Tectonics of the Appalachians*. New York, NY: Wiley-Interscience.

Rush, S., Klaus, N., Keyes, T., Petrick, J., & Cooper, R. (2012). Fire severity has mixed benefits to breeding bird species in the southern Appalachians. *Forest Ecology and Management*, *263*, 94–100.

Schaetzl, R., & Anderson, S. (2005). *Soils: Genesis and geomorphology*. Cambridge, UK: Cambridge University Press.

Scholes, M. C., & Nowicki, T. E. (1998). Effects of pines on soil properties and processes. In D. M. Richardson (Ed.), *Ecology and biogeography of Pinus* (pp. 341–353). Cambridge, UK: Cambridge University Press.

Simon, S. A. (2013). *Ecological zones on the George Washington National Forest: First approximation mapping* (Unpublished Report). The Nature Conservancy, Virginia Field Office.

Simon, S. A., Collins, T. K., Kauffman, G. L., McNab, W. H., & Ulrey, C. J. (2005). Ecological zones in the Southern Appalachians: First approximation. *Research paper SRS-41*. Asheville, NC: USDA Forest Service.

Ungerer, M. J., Ayres, M. P., & Lombardero, M. J. (1999). Climate and the northern distribution limits of Dendroctonus frontalis Zimmermann (Coleoptera: Scolytidae). *Journal of Biogeography*, *26*(6), 1133–1145.

USCESA. (1976). *U.S. standard atmosphere, 1976* (NOAA-S/T 76-1562). Washington, DC: US Government Printing Office.

USFS. (2014). *Revised land and resource management plan, George Washington National Forest* (R8-MB 143 A). Roanoke, VA: US Forest Service, Region 8.

Waldrop, T. A., & Brose, P. H. (1999). A comparison of fire intensity levels for stand replacement of table mountain pine (Pinus pungens Lamb.). *Forest Ecology and Management*, *113*(2–3), 155–166. doi:10.1016/S0378-1127(98)00422-8

Werner, H. J. (1966). *Geology of the Vesuvius Quadrangle, Virginia* (Report of Investigations 7). Charlottesville, VA: Virginia Division of Mineral Resources.

Whittaker, R. H. (1956). Vegetation of the great smoky Mountains. *Ecological Monographs*, *26*(1), 1–69.

Wilkes, G. P. (2002). *Geologic map of the virginia portion of the Lewisburg 30 × 60 minute quadrangle*. Charlottesville, VA: Virginia Division of Mineral Resources.

Williams, C. E. (1998). History and status of Table Mountain pine-pitch pine forests of the southern Appalachian Mountains (USA). *Natural Areas Journal*, *18*, 81–90.

Zar, J. H. (1999). *Biostatistical Analysis* (4th ed.). Upper Saddle River, NJ, USA: Prentice Hall.

Zobel, D. B. (1969). Factors affecting the distribution of Pinus pungens, an Appalachian Endemic. *Ecological Monographs*, *39*(3), 303–333.