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ORIGINAL PAPER

The influence of logging and topography on the distribution of spruce-fir forests near their Southern limits in Great Smoky Mountains National Park, USA

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Abstract We studied the effects of logging history, topography, and potential insolation on the lower-elevation limit of existing spruce-fir forest in Great Smoky Mountains National Park (GRSM). Dummy-variable regression, analysis of variance, and classification trees were applied to environmental data within a geographic information system framework. The effect of logging history on the lower limit of spruce-fir depended on aspect. On north-facing slopes (270°– 90°), the presence of spruce-fir was independent of both logging history and potential insolation. On south-facing sites (90°–270°), the elevation of spruce-fir was significantly higher (by 122 m) in areas that had been logged historically. Classification-tree models suggested an even greater logging effect, indicating that both the lower limit and the upper dominance zone of spruce-fir forest are, on average, nearly 200 m higher in historically logged landscapes. Presence of spruce-fir on south aspects was also significantly related to potential insolation, but the strength of this effect was not dependent on logging history. Classification-tree models, developed separately using data from logged sites versus unlogged sites, were used to estimate the current area of spruce-fir forest in the park expected under the hypothetical scenario that no spruce-fir had been logged (38,675 ha) versus the alternate scenario that it had hall been logged (11,727 ha). At present the area of spruce-fir forest in the park is 21,242 ha. We found greater prevalence of spruce-fir on the Tennessee side of the divide on south aspects and historically logged sites, possibly due to greater occurrence of westerly winds and associated cloud cover.

Keywords *Abies fraseri* · Disturbance · Ecotone · *Picea rubens* · Southern appalachians

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Introduction

The ecotone between higher elevation needle-leaved evergreen forests dominated by spruce (*Picea*) and fir (*Abies*) and lower elevation broad-leaved deciduous forests represents a major indicator of climate-vegetation relations in eastern North America (Delcourt and Delcourt 1984). In the Appalachian Mountains, this ecotone is found at successively higher elevations southward (Cogbill and White 1991), with the southernmost extent of these forests occurring at about 35° N latitude. Whittaker (1956) and others (cf. Delcourt and Delcourt 1984) have reported that the elevation of this ecotone has varied in the past, reaching a relatively low point at 18,000–12,000 years BP (<1,000 m elevation at 35° N) and a relatively high point during a postglacial temperature maximum about 5,000 years BP (>1700 m). Future climate changes will presumably continue to affect the position of this ecotone.

It is usually assumed that temperature, and therefore elevation and slope aspect, control the position of the spruce-fir ecotone. For example, several authors have reported that slope aspect modifies the effect of elevation per se and that the ecotone is approximately 200 m higher on warmer (southwest) slope faces (Schofield 1960; Sullivan 1993; White et al. 1993). However, environmental factors other than temperature may be important. To date, no multifactor analysis of the spruce-fir ecotone has been attempted despite the widespread interpretation of this ecotone as a major climatic signal.

Logging during the late 1800s and early 1900s caused dramatic change in the southern Appalachians, and post-logging fires and severe soil erosion were frequently reported (Pyle 1984; Pyle and Schafale 1988). Early logging was selective, with preference for red spruce due to its greater economic value (Korstian 1937). Later, clear cutting of trees ensued at all elevations to get every merchantable tree off the land. There were generally no long term management plans after cutting, and soils were not reworked or planted (Pyle 1984; Pyle and Schafale 1988). Logging and fire exposed the normally damp substrate of the spruce-fir forest and/or physically destroyed organic surface layers. Canopy removal and consequent increases in solar radiation would have elevated surface temperatures, dried out soils, reduced infiltration, and promoted soil erosion (Pyle and Schafale 1988).

These human disturbances lay well outside the historic range of variability of the spruce-fir ecosystem, which was characterized by small gap dynamics prior to logging (White et al. 1985), and widespread regeneration failure resulted (Korstian 1937, White et al. 2001). In this sense, spruce and fir are "foundation" species in this ecosystem—species whose physical characteristics (evergreen shade, slowly decomposing litter producing a thick mor humus) affect many species in the community, including their own ability to regenerate. The removal of these species, either directly or through the accompanying soil erosion, has exceeded the system's ability to recover in some areas, and logged and soil-eroded sites remain without spruce-fir forests some 70–100 years after logging. Thus, human disturbance has also altered the position of the spruce-fir ecosystem. By building models of the ecotone in both logged and unlogged sites within Great Smoky Mountains National Park (GRMS) we can estimate the net reduction in the extent of this ecosystem with logging.

Spruce-fir forests are one of the rarest and most threatened ecosystems in the southeastern United States (Noss et al. 1995; White and Miller 1998). Appalachian montane spruce-fir forests are distinct from boreal forests in that the Appalachian spruce is *Picea rubens* Sarg. (*Picea glauca* (Moench) Voss and *Picea mariana* (Mill.) B.S.P. in the boreal forest) and the disturbance regime is dominated by wind, with natural fires absent. The southern Appalachian spruce-fir forests are further distinct from northern Appalachian forests in that the fir is *Abies fraseri* (Pursh) Poir. (a narrow endemic; *Abies balsamea* L. occurs in the northern Appalachians and boreal forest), precipitation is higher (but snow fall is lower) and there is a sizeable gap in well developed spruce-fir forests between New York and Virginia because the appropriate elevation for this ecosystem is rarely reached. The southern Appalachian spruce-fir forests have approximately a 57% floristic similarity with those of the northern Appalachians (White and Miller 1993). The southern Appalachian spruce-fir forests have attracted considerable research attention, partly due to their disjunct distribution (Whittaker 1956), rare species (White and Miller 1988), and sensitivity to air pollution, climate change, and disease (Busing and Pauley 1994; Smith and Nicholas 1998).

We used remote sensing and digital terrain maps, to produce the first rigorous analysis of the ecotone position in GRSM near the southernmost extent of these forests in eastern North America. The establishment of GRSM protected the largest extant block of old growth spruce-fir forests in the southern Appalachians. Despite evidence that the lower limit of spruce-fir in GRSM is controlled by climate and anthropogenic disturbance, the individual and interactive effects of these factors have not been directly evaluated.

Methods

For the spatial distribution of spruce-fir forests within GRSM we used a vegetation map produced jointly by the US Forest Service, US Geological Survey, US Environmental Protection Agency, and Pacific Meridian Resources, Inc. for the Southern Appalachian Man and Biosphere program. The vegetation map was produced at 30 m spatial resolution using a combination of aerial photographs, field plots, and satellite data from Landsat Thematic Mapper (TM). The TM pixels were classified as evergreen forest if total tree cover exceeded 25%, and if at least 70% of the tree-crown cover was evergreen. Spruce-fir forest was separated from the other two evergreen classes (white-pine/hemlock and southern yellow pine) based on reflectance characteristics. Map accuracy was assessed using aerial photographs and over 200 field samples (SAMAB 1996; Dull et al. 1988). Maps of logging history for GRSM were provided by the National Park Service. These maps are based on the work of Pyle (1984). Note that some logged areas burned and some didn't, and locations that are mapped as logged would have included some areas that loggers never got to for one reason or another.

Elevation data from a USGS 30-m digital elevation model (DEM) was used to model potential solar insolation, and as surrogate data for precipitation, temperature, and cloud prevalence. In general, precipitation increases, cloud cover increases, and temperature decreases with increasing elevation in GRSM (Shanks 1954; Dickson 1959; Schofield 1960). The DEM also was used to derive slope aspect and to partition samples into two general exposure classes: north aspect (sites with aspects between 270 and 90°) and south aspect (sites with aspects between 90 and 270°).

Potential at-surface irradiance for clear-sky conditions was derived from the DEM using the model of Kumar et al. (1997). This model uses sun-slope geometry to derive solar elevation and azimuth angles relative to the slope and aspect of each pixel. The model accounts for shadowing due to adjacent terrain and changes in beam attenuation related to sun angle. Using these methods, we produced a spatially distributed field of average potential April insolation (PI, $W \cdot m^{-2}$) for GRSM.

A regular grid of 1 km^2 cells was used as a frame from which to extract samples for data analysis. The grid was oriented north-south, and a buffer was generated to extend 1 km above and below the mapped boundary of the spruce-fir forest. Sample points were located at the center of each 1 km^2 grid cell that fell within the 2 km buffer zone (Fig. 1). The 1 km grid-cell spacing was chosen to reduce spatial dependence among samples. The 1 km buffer was used so that samples would be constrained to areas immediately on either side of the spruce-fir boundary. In this way, we attempted to avoid spurious results that would arise if samples were selected from well above, or well below the boundary.

A total of 407 grid cell centers fell within the 2 km buffer zone. Due to the shape and size of the spruce-fir distribution in GRSM, the area of the 1 km buffer below the spruce-fir boundary was greater than the area above the boundary; for example in areas where spruce-fir is distributed along narrow ridges. Thus there were a greater number of samples, at which spruce-fir was absent (255) as opposed to present (152). Five variables were determined for the 30 m pixel containing each sampled point; presence/absence of spruce-fir, logged/unlogged, south/north aspect, elevation, and PI.

We used t-tests, ANOVA, and multiple-regression with dummy variables to test the simple and interacting effects of climate and logging on the modern distribution of spruce-fir in GRSM. A significance criteria of α=0.05 was used for all statistical analyses. Specifically, we tested the following hypotheses:

H1: Spruce-fir is restricted to increasing elevations along a gradient from low to high PI.

H2: The strength of any effect identified in **H1** depends on logging status.

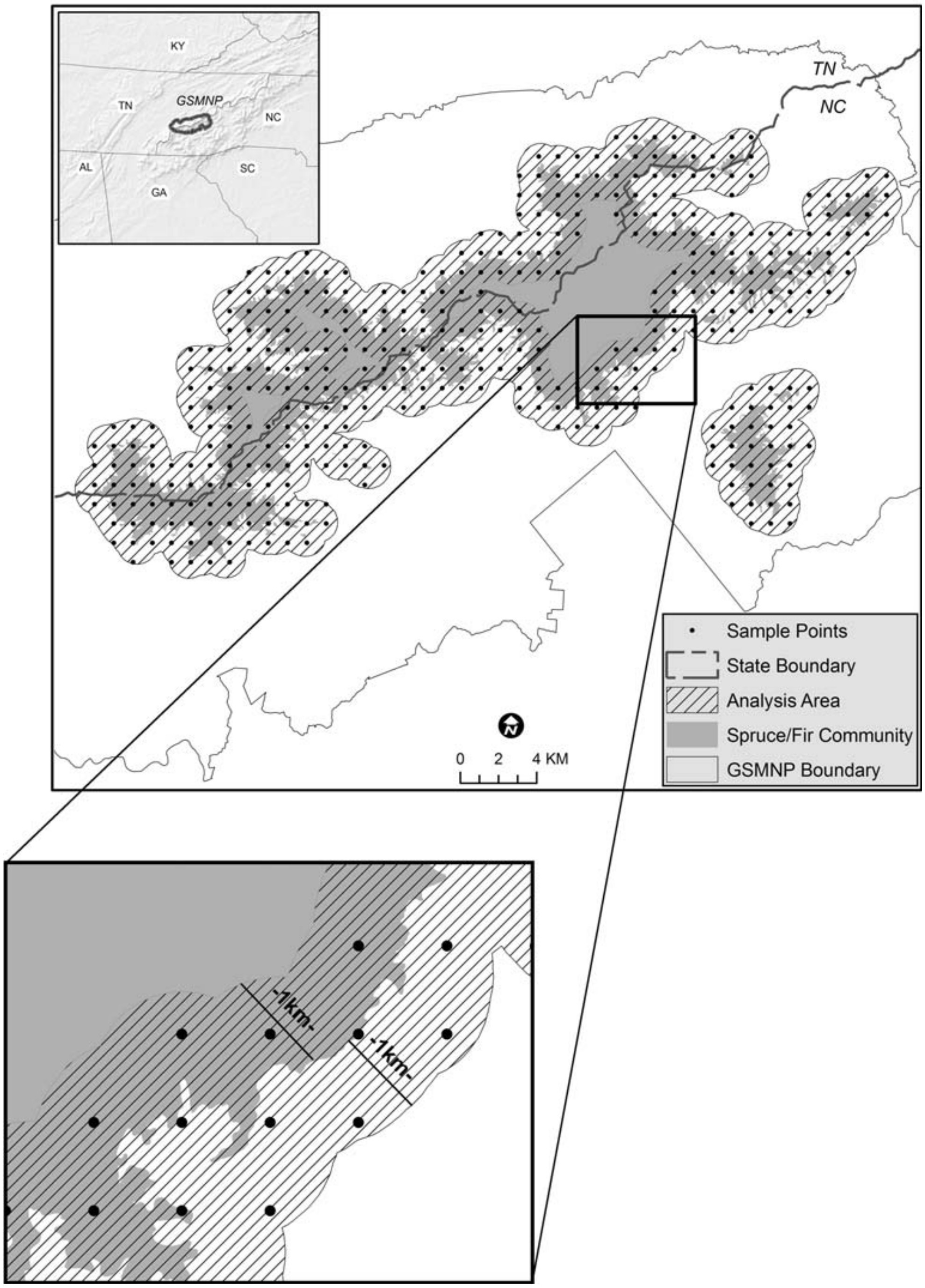

Fig. 1 Eastern portion of GSMNP. Samples were constrained within a 2 km buffer centered on the lower limit of the mapped spruce-fir distribution. Within this buffer zone, a regular 1 km grid was used to identify sample sites. Analysis was based on 30 m data extracted for each sample site

H3: The strength of the effects identified in **H1** and **H2** depend on general aspect (N/S).

A premise underlying these hypotheses is that if surface temperature, through its control over soil moisture, influences the lower limits of spruce-fir forest, then interactions between elevation and insolation should be evident in the data. That is, spruce and fir, which are known to require moist conditions for germination and seedling survival, should be found at increasingly higher elevations on increasingly exposed slopes.

Classification tree models were developed as an alternative method to examine the influence of elevation and insolation on the presence of spruce-fir, and as crude predictive models for estimating geographic distributions of spruce-fir expected under the hypothetical scenario that no spruce-fir had been logged (unlogged scenario) versus the alternate scenario that it had hall been logged (logged scenario). Classification trees are nonparametric models that are fit by recursively partitioning a response variable (in our case the response is binary, i.e. presence/absence) into increasingly uniform subsets by splitting the data on critical thresholds in continuous or categorical predictor variables (De'Ath 2002). The relative importance of predictor variables, nonlinear relationships, and variable interactions are exposed in the structure of the tree. Tree models can be graphically illustrated so that a progression of binary splits on the independent variables leads to a prediction at an end node (e.g. see Fig. 5). The predicted value at a given end node is the most commonly occurring state among the set of observations that are channeled through the tree to that node. For our purposes classification trees were limited to no greater than four splits in order to avoid overfitting the models to the data.

In addition to the variables described above, other factors, such as general climate patterns or fire history could influence the distribution of spruce-fir in GRSM. To explore the effects of these factors, we compared sample sizes, and percentage of sites with spruce-fir present, for all combinations of aspect and logging history separated by burn history (burn versus no burn) and state (Tennessee versus North Carolina). Since the boundary between TN and NC follows the Appalachian divide, separating by state accounts for differences in orientation relative to the prevailing westerly winds, which may lead to greater cloud cover on the Tennessee side of the park. Considering burn history and state also allowed us to quantify differences in the rate of spruce-fir presence under a greater variety of settings. However, we did not use these data in the statistical analyses described above because of limits in degrees of freedom, and because our primary interest was in the legacy of logging as an historical land use.

Results

Approximately the same number of samples sites fell on north and south aspects (214 and 193, respectively). A disproportionate number of the sites were unlogged, especially where spruce/fir was present (Table 1). As noted above, spruce-fir was absent at more sites than it was present. This difference was especially notable on south aspects, on sites that had been logged (Table 1), and on the NC side of the divide (70% absent in NC versus 52% absent in TN).

There was no statistical difference in the mean elevation of logged versus unlogged sample points, suggesting that, within the 2 km buffer, elevation and logging status were independent. This was the case regardless of whether spruce-fir was present. As expected, the mean elevation of sites was significantly higher where spruce-fir was present rather than absent (t=15.27; P>t=0.000). This effect was predetermined by the sampling design and study objectives, and reflects the elevational zonation of plant communities at the spruce-fir boundary. The average potential insolation (PI) was significantly lower for sites at which spruce-fir was present (t=–2.10; P>t=0.04).

Considering only logged sites, the mean elevation of the spruce-fir ecotone was significantly

Table 1 Number of sites, under each combination of logging history and general aspect, with spruce-fir present and absent (present/absent) there were 407 sites in total

Status	All	North	South
Logged & Unlogged	152/255	90/124	62/131
Logged	34/131	18/65	16/66
Unlogged	118/124	72/59	46/65

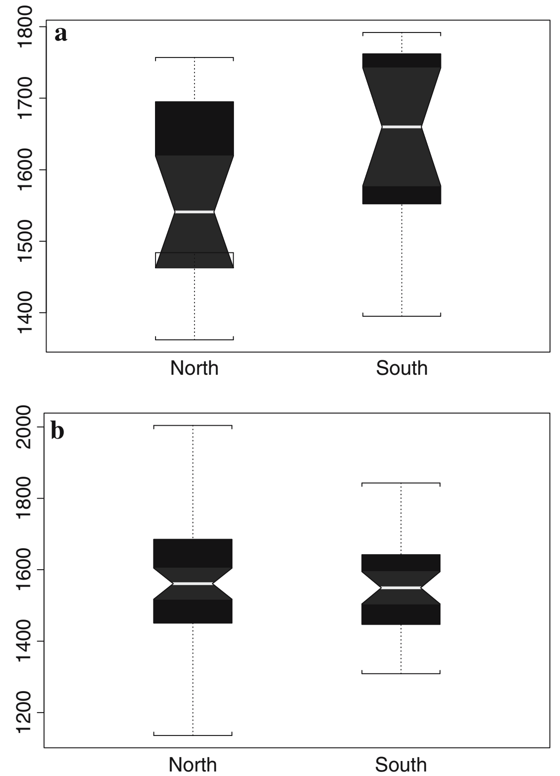

Fig. 2 Boxplots showing elevation distributions for north-aspect versus south-aspect sites where spruce-fir was present. **a** logged sites (t=2.49; P>t=0.03), **b** unlogged sites

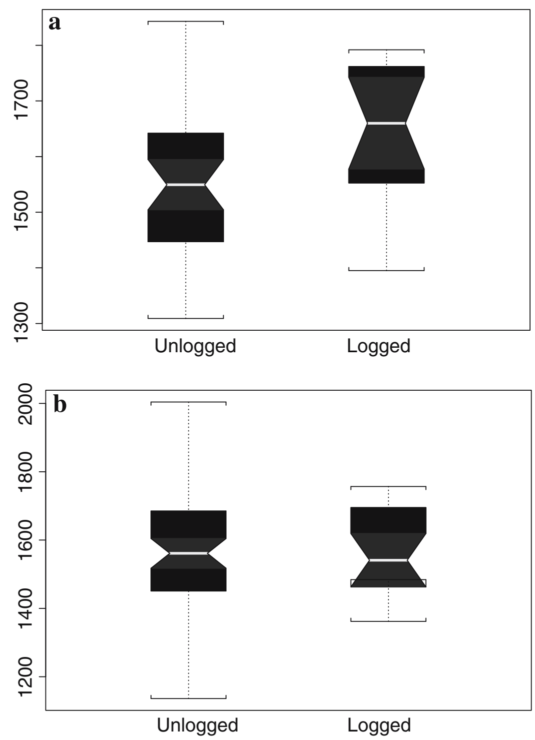

Fig. 3 Boxplots showing elevation distributions for logged vs. unlogged sites where spruce-fir was present. **a** south-facing (t=2.68; P>t=0.01), **b** north-facing.

higher on south vs. north aspects (t=2.49; P>t=0.03) (Fig. 2a). However, no such difference occurred for unlogged sites (Fig. 2b). Likewise, when only south-facing slopes were considered, the mean elevation of the spruce-fir ecotone was significantly higher on logged landscapes vs. unlogged landscapes (t=2.68; P>t=0.01) (Fig3a). For north facing slopes, the elevation of the spruce-fir ecotone did not differ by logging status (Fig. 3b).

The relationship between PI and the elevation of the spruce-fir ecotone depended on logging status and general aspect (Fig. 4). There was no relationship between insolation and elevation on north-facing slopes, regardless of logging status. However, for unlogged, south-facing sites, we found a significant positive relationship between PI and the elevation of the spruce-fir ecotone (r=0.43; t=2.37; P>t=0.03). On logged south-facing sites the correlation between these two variables was substantially greater (r=0.78; t=3.52; P>t=0.008). Despite this increase in correlation, the slope of the relationship between elevation and PI for logged, south-facing sites was not statistically greater than the slope term for unlogged sites (increase in slope term = 10.78; t=1.64; P>t=0.11). Thus the slope term associated with logging was omitted from the dummy variable regression model. The remaining intercept term for logging was significant, and indicated an increase of 122.6 m in the mean elevation of the spruce-fir ecotone due to historical logging on south-facing slopes (Table 2).

The classification accuracies (number of sites correctly classified/total number of sites) were 88 and 81% for the logged and unlogged classification tree models, respectively. The model based on unlogged site data indicates that spruce-fir nearly always occurred above 1513 m (upper dominance zone), and never occurred below 1285 m (lower limit) (Fig. 5a). The model developed from logged sites produced corresponding values of 1698 m and 1482 m (Fig. 5b) reflecting a 197 m upwards shift of the lower limit, and a

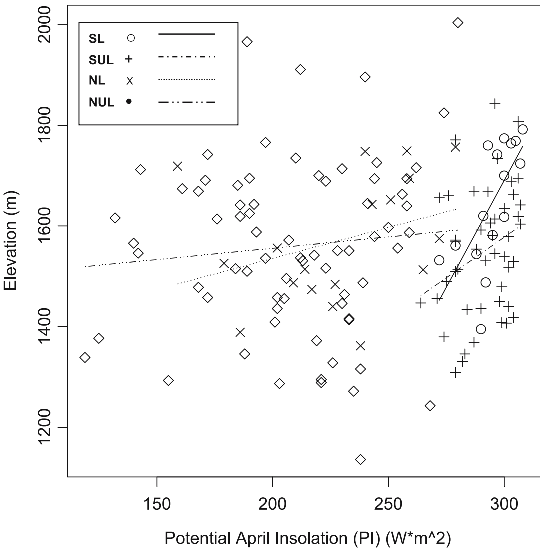

Fig. 4 Regression model results summarizing the association between PI and elevation at sites for which spruce-fir was present. General aspect (N/S-facing) and logging status were included as dummy variables. The regression lines in this graph are from the full model which included slope and intercept terms for both dummy variables. The final model, which included only significant terms, is presented in Table 2. For north aspects, none of the slope terms were significantly greater than zero for either logged or unlogged cases. On south aspects there was a significant relationship between the amount of radiation received and the elevation of the spruce-fir ecotone. The difference in the slope-term associated with logging on south-aspects was not significant, but the intercept was, indicating an increase of 122.5 m in the lower limit of spruce-fir associated with historical logging on south-facing sites. SL = Logged South Facing, SUL = Unlogged South Facing, NL = Logged North Facing, NUL = Unlogged North Facing

185 m shift of the upper dominance zones for logged sites relative to unlogged sites. In both models, the presence of spruce-fir at elevations

Table 2 Regression results of Elevation (elevation of the spruce-fir ecotone) on PI and logging-status

Model term	Coefficient	Standard error	*t* value	P(>|*t*|)
Intercept	49.7	497.4	0.099	0.92
PI	5.07	1.68	3.02	0.005
Logging Status	122.553	38.15	3.21	0.003

Logging status was included as a dummy variable to account for the intercept effect. The coefficient for logging status (122.6) suggests that logging increased the lower limit of spruce-fir by 122.6 m on south aspects. The slope effect of logging status, though suggestive, was not significant at α=0.05, and was omitted from the model. Model summary: R^2=0.41; F=12.03; P >F=0.0001

between the lower limit and the upper dominance zone either depended on radiation (PI), or on an interaction between radiation and elevation (Fig. 5).

The classification tree models were used to map the expected distributions of spruce-fir under two historical disturbance scenarios: all lands logged and no lands logged (Fig. 6a, b). The lands currently mapped as spruce-fir forest in the coverage used for this analysis occupy approximately 21,242 ha. The distributions predicted under the logged and unlogged scenarios using the regression tree models covered approximately 11,727 ha and 38,675 ha, respectively. Note from Fig. 6a that some areas which remained unlogged were predicted to contain spruce-fir based on the unlogged model, and yet do not contain spruce-fir. These areas are mostly distributed on the NC (south) side of the park and the east end of the park.

Of the 407 sample sites, 65 (16%) were recorded as having burned historically. Of these, 54 (83%) had also been logged. Spruce-fir was present on less than 22% of burned sites, regardless of logging history and aspect. Unexpectedly, for sites that had been both logged and burned, spruce-fir was present at nearly twice the rate on south aspects (21% or 6 of 28 sites) than on north aspects (11% or 3 of 26 sites). On sites that had not burned, spruce-fir presence varied strongly with aspect and logging history as indicated by the results described above. Among unburned sites, spruce-fir was present to a consistently higher degree on north aspects and on unlogged sites, ranging from 19% on logged, south-facing sites, to 56% on unlogged, north-facing sites (Table 3).

Because, the Tennessee side of GRSM faces the prevailing westerly winds, sample sites in Tennessee may be subject to greater cloud cover than those in North Carolina. This raises the possibility of an additional confounding factor in our analyses, or bias if there was an uneven distribution of logged versus unlogged, or north- versus south-facing sites across the two states. North-facing sites were split approximately evenly (48 and 52% for NC and TN, respectively), while more south-facing sites occurred in NC than in TN (63 and 37%, respectively). Spruce-fir was

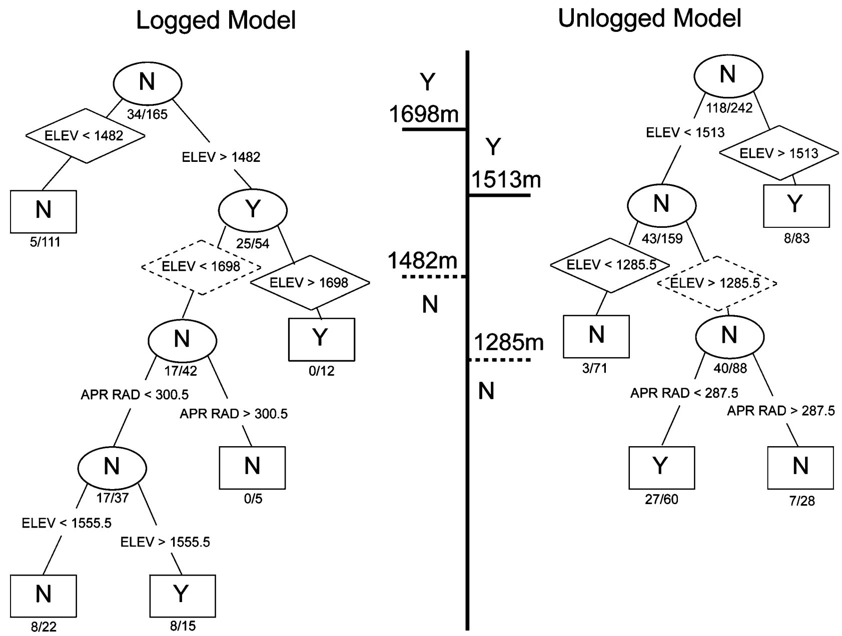

Fig. 5 Classification trees built using logged and unlogged sample sites separately. Ovals and squares represent nonterminal and terminal nodes, respectively. The *Y*/*N* values inside the ovals and squares are the predictions of presence (*Y*) or absence (*N*) of spruce-fir for all samples that are routed through the tree to any particular node. The ratio values beneath ovals and squares are misclassification rates at each node. Critical thresholds are displayed along the arcs between the nodes. These are the split values that provide the basis for making predictions. The variable abbreviations are ELEV = elevation; APRRAD = April potential insolation. Solid bold diamonds and horizontal line segments indicate the predicted elevation of the lower limit of the upper dominance zone. Dashed diamonds and line segments indicate the predicted lower limit of spruce-fir. Below the dashed diamonds the presence of spruce-fir depends on APRRAD

present at a roughly equal rate on unlogged, north-aspect sites (54 and 56% for TN and NC, respectively). However, for all other combinations of aspect and logging history, spruce-fir was more frequently present in Tennessee and, for logged sites, was twice as frequent in Tennessee than in North Carolina, regardless of aspect (Table 4).

Discussion and Conclusions

Previous studies have shown that the lower limit of spruce-fir forest in GRSM is substantially higher on south- versus north-facing slopes (Schofield 1960; Sullivan 1993; White et al. 1993), as suggested in our hypothesis H1. This pattern was present in our data, but depended on logging history as per our H2. Only on logged, south-facing sites was the mean elevation of spruce-fir significantly higher than on any other combination of logging and aspect, thus supporting our hypotheses H2 and H3. The effect of logging is statistically detectable only on south aspects, and indicates a 122 m increase in the average elevation of spruce-fir associated with logging on south aspects. Classification-tree models suggested stronger effects, identifying average increases of nearly 200 m in both the lower limit and the upper dominance zone of spruce-fir associated with historical logging in GRSM. Our results imply that the average elevation of the spruce-fir lower limit on logged south-facing slopes was below its current position prior to logging, and that these sites were less suitable than north-facing sites for the recovery of spruce-fir forest. Our findings also suggest that, prior to logging, the spruce-fir distribution depended primarily on elevation,

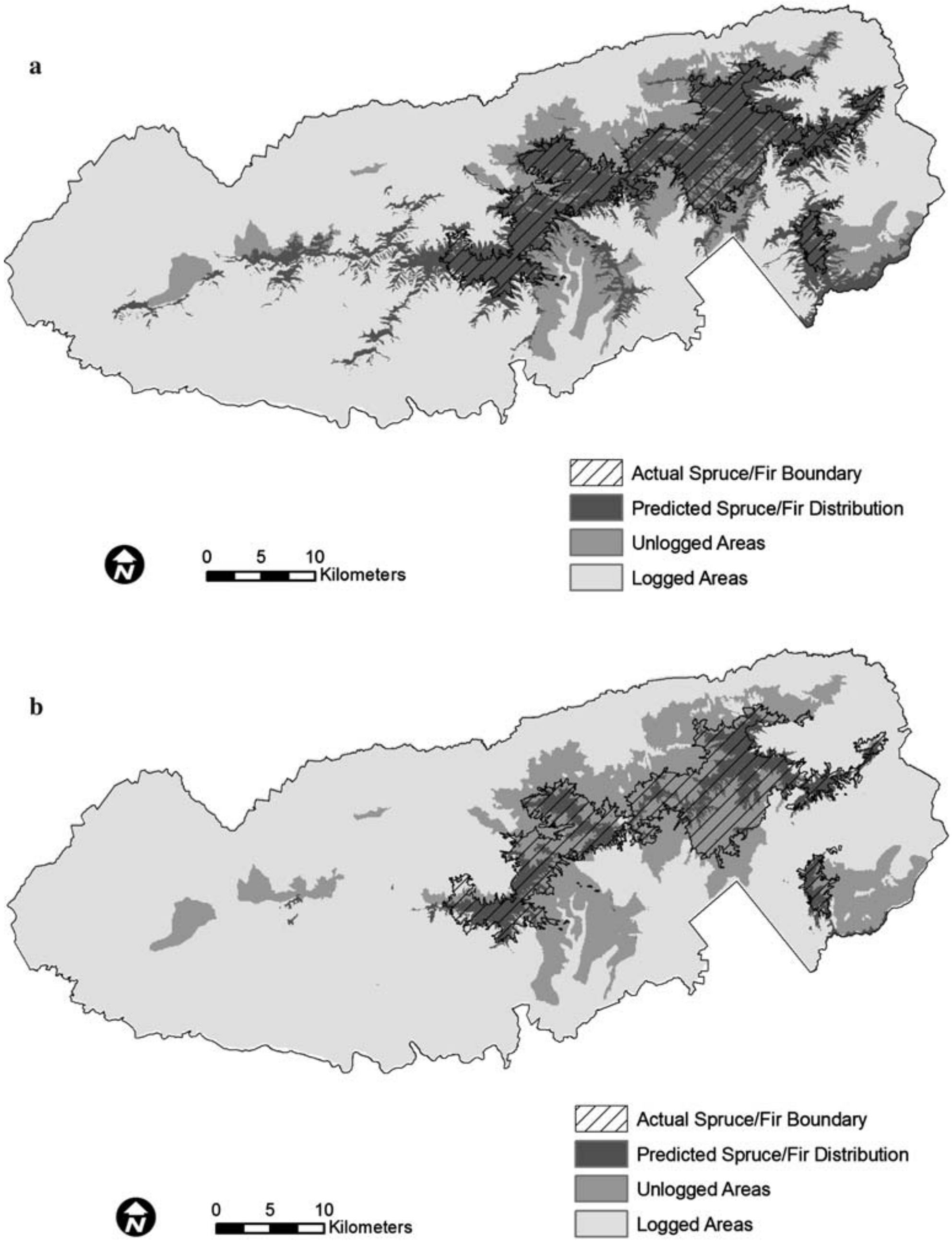

Fig. 6 Geographic distributions of spruce-fir in GSMNP modeled using the classification trees shown in Fig 5 for **a** unlogged and **b** logged scenarios. The current distribution of spruce-fir and historical logging data are also shown in these maps for comparison

a determinant of orographic gradients in temperature, moisture, and cloud cover, and, with the exception of the most exposed sites, was not strongly influenced by general aspect.

One possible explanation for the observed patterns is that logging, by disturbing and exposing soil and litter surfaces to direct solar radiation and wind, resulted in modifications of

Table 3 Percentage of sites with spruce-fir present under all combinations of logging history, fire history, and general aspect

Spruce-fir present	Unburned			Burned		
	North	South	N/S	North	South	N/S
Logged	26% (57)	19% (54)	23% (111)	11% (26)	21% (28)	17% (54)
Unlogged	56% (126)	43% (105)	50% (231)	20% (5)	17% (6)	18% (11)

Numbers in parentheses indicate the total number of sites for each combination of factors. For example, there were 57 logged, unburned, north-facing sites in total. Spruce-fir was present at 26% of these

Table 4 Percentage of sites with spruce-fir present under all combinations of logging history, general aspect, and TN versus NC location

Spruce-Fir Present	Tennessee			North Carolina		
	North	South	N/S	North	South	N/S
Logged	30% (20)	35% (20)	33% (40)	19% (63)	15% (62)	17% (125)
Unlogged	54% (83)	50% (51)	52% (134)	56% (48)	35% (60)	44% (108)
Logged/Unlogged	50% (103)	46% (71)	48% (174)	35% (111)	25% (122)	30% (233)

Numbers in parentheses indicate the total number of sites for each combination of factors. For example, there were 83 unlogged, north-facing sites in Tennessee. Spruce-fir was present at 54% of these

surface-energy balance and water budgets that directly inhibited recovery of spruce-fir (Pyle 1984; Pyle and Schafale 1988). In this energy/water-balance scenario, south-facing sites that, prior to logging, were probably maintained in spruce-fir through gap-phase succession (White et al. 1985), would have experienced evaporative losses in soil moisture sufficient to limit spruce-fir regeneration in the cut-over landscape. At such sites, cool, moist conditions necessary for recruitment of spruce and fir, would only return with either anomalous climate conditions or establishment of a canopy by species that are more suitably adapted to regenerate on exposed sites. By the time such conditions occur, ecological processes, such as dispersal limitation, or competition in the ground layer, could continue to preclude recruitment of spruce-fir in canopy gaps. The results from the dummy-variable regression, which showed that the lower elevation of spruce-fir on south-facing slopes depended on radiation load, lend further support to an energy/water-balance interpretation of the observed patterns by suggesting that spruce-fir is sensitive to radiation load at exposed sites.

Alternate interpretations of the observed patterns relate to environmental factors, such as fire or soil erosion, that could be disproportionately at play on logged, south-facing slopes. In our fire data, the 54 sites that burned were split evenly between north- and south-aspects. Spruce-fir was rarely present on these sites, regardless of aspect or logging history, suggesting that the impact of burning on spruce-fir superceded the effects of aspect, logging, and any interactions between them. Nevertheless, some fires may have been unrecorded or inaccurately mapped, and it is possibile that south-facing slopes were more likely to burn after logging than their north-facing counterparts. Disturbance and exposure due to logging and burning of spruce-fir often promoted soil erosion (Whittaker 1956), which, possibly because of topoclimatic factors, could also have been more severe on south aspects, and thus disproportionately reduced spruce-fir regeneration at these sites.

It has been argued that climatic factors associated with cloud cover control the spruce-fir ecotone in New England (Siccama 1974). In our study area, the percentage of sites with spruce-fir present was approximately equal on the Tennessee and North Carolina sides of the divide for unlogged north-aspect sites, but consistently higher on the Tennessee side for logged and/or south-aspect sites. This suggests that orientation towards the prevailing westerly winds, which could produce a greater prevalence of cloud cover on the Tennessee side of the divide, may have helped moderate post-logging conditions enough to improve recolonization by spruce-fir after logging, and to increase the prevalence of spruce-fir on south-facing sites, relative to the North Carolina side.

The energy/water-balance scenario suggested above implies that, at more stressful locations, the presence of spruce-fir at its lower limit depends partly on a biophysical feedback between the plant canopy and climate. Where prevailing climate is suitable (e.g. on north aspects, or under sufficient cloud cover) spruce-fir has a greater likelihood of re-establishment after logging. Where conditions are too dry regardless of canopy cover, spruce-fir will not establish, and any relictual stands from past climate phases will die out. Between these two states is a third, in which the forest composition and surface climate are mutually stabilizing. In these areas, prevailing climate may, at times, be out of phase with the life-history adaptations of spruce-fir, but the community can persist by virtue of the canopy influence on surface energy- and water balance. This feedback between the plant canopy and the climate within the spruce-fir recruitment environment leads to a dynamic stable state for the ecosystem when the disturbance regime produces small isolated canopy gaps, but is disrupted by an extensive, severe disturbance such as fire or logging. This scenario can be interpreted more broadly, and considered in relation to theoretical concepts regarding disturbance, landscape legacies, ‘‘foundation’’ species, and community stability.

Disturbance that produces conditions outside the historic range of variability for an ecosystem can potentially disrupt regulatory biophysical feedbacks beyond critical thresholds, thus releasing the system to evolve a new stable state (*sensu* Petraitis and Latham 1999). This system-collapse scenario results from changes in biotic, abiotic, and/or ecological processes and conditions brought about either directly or indirectly by the disturbance. In their discussion of alternate stable community states, Petraitis and Latham (1999) used the example of North American heathland/forest mosaics, where patches of heathland and forest vegetation were taken to represent new stable community states, and transitions between them were initiated by severe fire and drought or clearcutting (forest to heathland) or fire suppression and nutrient addition (heathland to forest).

In the case of spruce-fir in GRSM, the historic range of variability in ecosystem conditions due to disturbance is at the scale of small canopy gaps (White et al. 1985). Spruce-fir forests were typically unaffected by wildfire, which was generally restricted to lower elevations (Korstian 1937). Thus, logging can produce conditions that are well outside the historic range of variability for the system. Our results suggest that logging may have disrupted the moderating influence of the canopy on the spruce-fir recruitment environment beyond the critical threshold for recovery on south-facing slopes, especially on the NC side of the divide. As has been described in several studies of inter-species facilitation (Bertness and Callaway 1994; Hacker and Gaines 1997; Tewksbury and Lloyd 2001), the importance of the biophysical interaction (moderation of the subcanopy climate by the spruce-fir canopy) to the regeneration and long-term stability of the extant community (spruce-fir) appears to differ across the stress gradient, with the greatest effect where abiotic stress is highest.

Although based on comparative observation, rather than experimental evidence, our results appear to reflect the consequence of management practices that produce conditions outside the historic range of variability for the ecosystem. Management of this nature generates changes in environmental conditions that can disrupt ecosystem stability and lead to new stable community states, particularly at the more ecologically stressful portions of a community’s distribution. This framework suggests elements of a protocol for ecosystem management that would explicitly consider the historic range of variability in environmental conditions due to disturbance, critical thresholds on limiting environmental factors at different life-history and successional stages, and potential new stable community states.

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