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Site characteristics of red spruce witness tree locations in the uplands of West Virginia, USA

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THOMAS-VAN GUNDY, M. (Northern Research Station, USDA Forest Service, PO Box 404, Parsons, WV 26287), M. STRAGER, AND J. RENTCH (West Virginia University, Division of Forestry and Natural Resources, Morgantown, WV 26506-6125), Site characteristics of red spruce witness tree locations in the uplands of West Virginia, USA. J. Torrey Bot. Soc. 139: 391–405. 2012.—Knowledge, both of the historical range of spruce-dominated forests and associated site conditions, is needed by land managers to help define restoration goals and potential sites for restoration. We used an existing digital database of witness trees listed in deeds from 1752 to 1899 to compare characteristics of red spruce (*Picea rubens* Sarg.) sites to non-red spruce sites to gain an understanding of historical spruce-dominated forests in West Virginia. The analysis revealed that red spruce witness trees were found at significantly higher elevations than non-spruce witness trees across the study area. However, spruce witness trees in the Western Allegheny Mountains subsection were found at significantly lower elevations than non-spruce witness trees. Indicator species analysis determined red spruce to be associated with toe slopes, benches, and valleys, although most locations were on side slopes. Across the entire study area, red spruce witness trees were more likely to be found on northeastern aspects and on acidic and frigid soils of the Mandy series. Historically, red spruce was associated with American beech (*Fagus grandifolia* Ehrh.), birch (*Betula* L.), and hemlock (*Tsuga canadensis* (L.) Carrière). This information should be used to guide red spruce restoration efforts and shows that a range of ecological settings should be considered when setting goals and implementing active management.

Key words: historical biogeography, indicator species analysis, *Picea rubens*, restoration ecology.

Restoration of the red spruce (*Picea rubens* Sarg.) and spruce-northern hardwood forests is a priority for the Monongahela National Forest (MNF) as expressed in the creation of a separate management prescription for restoration of spruce-dominated forests (USDA 2006). In these areas, restoration of spruce-dominated forests includes an increase in spruce dominance in the overstory and an increase in extent across the landscape through actions such as release of understory spruce, planting spruce seedlings, and group selection harvest to promote multiple age classes (USDA 2006). The broad goals for this MNF management prescription are: 1) maintaining or enhancing the spruce component within mixed spruce-hardwood communities, 2) restoring a spruce component to stands that contain understory spruce or scattered overstory spruce, and 3) restoring a multi-age structure in forests where spruce is being restored, enhanced, or maintained (USDA 2006). The desire to restore these forests is due, in part, to their extensive reduction in historic extent and the need to expand and connect rare species habitat. The success spruce has exhibited in regenerating naturally bodes well in its future recovery (Koon 2004, Nowacki et al. 2010).

The former extent of spruce-dominated forests in West Virginia is estimated from 600,000 to 900,000 ha (Hopkins 1899, Stephenson 1993). Early 20th century exploitative logging and subsequent fires in the spruce and spruce-northern hardwood forests changed microsite conditions drastically and reduced these forests to about 300,000 ha by 1865, 90,000 ha by 1899 (Hopkins 1899), and approximately 24,000 ha by the 1990s (Stephenson 1993). With thin bark, shallow roots, and non-serotinous cones, individual spruce are ill-adapted to fire. In addition, spruce occurs in landscape positions that rarely perpetuate surface fire, being cool, moist, and often shrouded in clouds or fog. Consequently, early 20th century fires that occurred in logging slash had long-lasting negative impacts.

These cool, moist, high-elevation, spruce-dominated forests support a number of rare species. These include the federally endangered

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Virginia northern flying squirrel (*Glaucomys sabrinus fuscus)*, the federally threatened Cheat Mountain salamander (*Plethodon nettingi*), snowshoe hare (*Lepus americanus)*, balsam fir (*Abies balsamea* (L.) Mill.), and bunchberry (*Cornus canadensis* L.). This forest type also adds to regional diversity by providing habitat for a combination of northern (e.g., hobblebush [*Viburnum lantanoides* Michx.] and mountain ash [*Sorbus americana* Marsh.]) and southern plant species (e.g., southern mountain cranberry [*Vaccinium erythrocarpon* Michx.]).

Knowledge of the historical range of spruce-dominated forests and associated site conditions is needed by land managers to help define restoration goals and potential sites for restoration. Quantitative information on historical forest conditions is sparse for much of the eastern United States due to early settlement and forest clearing by Europeans, and intensive timber harvesting early in the 20th century. Nevertheless, qualitative assessments of early forests and grasslands are useful in restoration ecology and can come from many sources such as land survey records, traveler's accounts, and photographs (Whitney 1994).

An existing digital database of witness trees listed in deeds from 1752 to 1899 was available to aid in restoration efforts on the MNF. In the absence of large old-growth forests, these historical references are often the best source of information on forest characteristics at the time of European settlement. Unlike in the Midwest, systematic grid-based surveys were uncommon in the original colonies. Here, land transfers followed survey methods called metes and bounds consisting of a series of bearings and distances with trees, posts, rock piles, or natural features recorded to describe corners where survey bearings changed. The numbers, species, and sizes of trees to record for each corner or point were not standardized and choice of witness tree was left to the discretion of the surveyor. Deeds or grants documenting transfer of ownership of a land parcel also document tree species existing at the time of transfer through these witness trees.

Witness tree data give a static "snapshot" of forest composition at the time of early European settlement. Witness trees have been used to describe European settlement-era vegetation of eastern forests (Abrams and Ruffner 1995, Black and Abrams 2001a, Black and Abrams 2001b, Whitney and DeCant 2003, Rentch and Hicks 2005). As such, relationships between vegetation and site conditions can be determined through analysis of witness tree locations on the landscape (Abrams and McCay 1996, Black and Abrams 2001a, Wang 2007). Witness tree data have been used to document changes in species composition and in particular, to address the apparent reduction in dominance by oak (*Quercus*) in current forests (Abrams and McCay 1996, Rentch and Hicks 2005) and other changes in forest conditions (Dyer 2001, Whitney and DeCant 2003, Wang et al. 2009). Species abundance may also provide information on historic disturbance regimes. When combined with archeological data, witness tree information can also reveal Native American influences on forest composition and structure (Black et al. 2006).

Surveyor bias toward certain tree species has been addressed in witness-tree studies based on Government Land Office methods (Bourdo 1956, Liu et al. 2011) and metes and bounds methods (Black and Abrams 2001a). Unusual tree species may have been more likely to be used as witness trees, as evidenced in Public Land Survey records in Wisconsin (Liu et al. 2011), as these would have made corners easier to re-locate. Longer-lived species would likely have been chosen over others, where available. Even though the choice of species to record as a witness tree was ultimately made by the surveyor, species occurrence is largely constrained by site factors so that even if bias existed, the mapping of vegetation at a landscape scale should not be significantly affected (Manies and Mladenoff 2000).

In the 1930s, USDA Forest Service personnel obtained from county courthouses copies of the first land grants or deeds for parcels that would later become the MNF. The bearings and distances listed in the deeds and land grants were then used by MNF staff to plot the parcels. In 2005, the 1930s paper maps were scanned and geo-referenced in GIS to preserve the information, making it electronically available for use and analysis. The creation of the witness tree database involved digital scanning of paper maps, manual digitizing of corner point locations, and transcription of tree species by corner from the associated deed (Thomas-Van Gundy and Strager 2012).

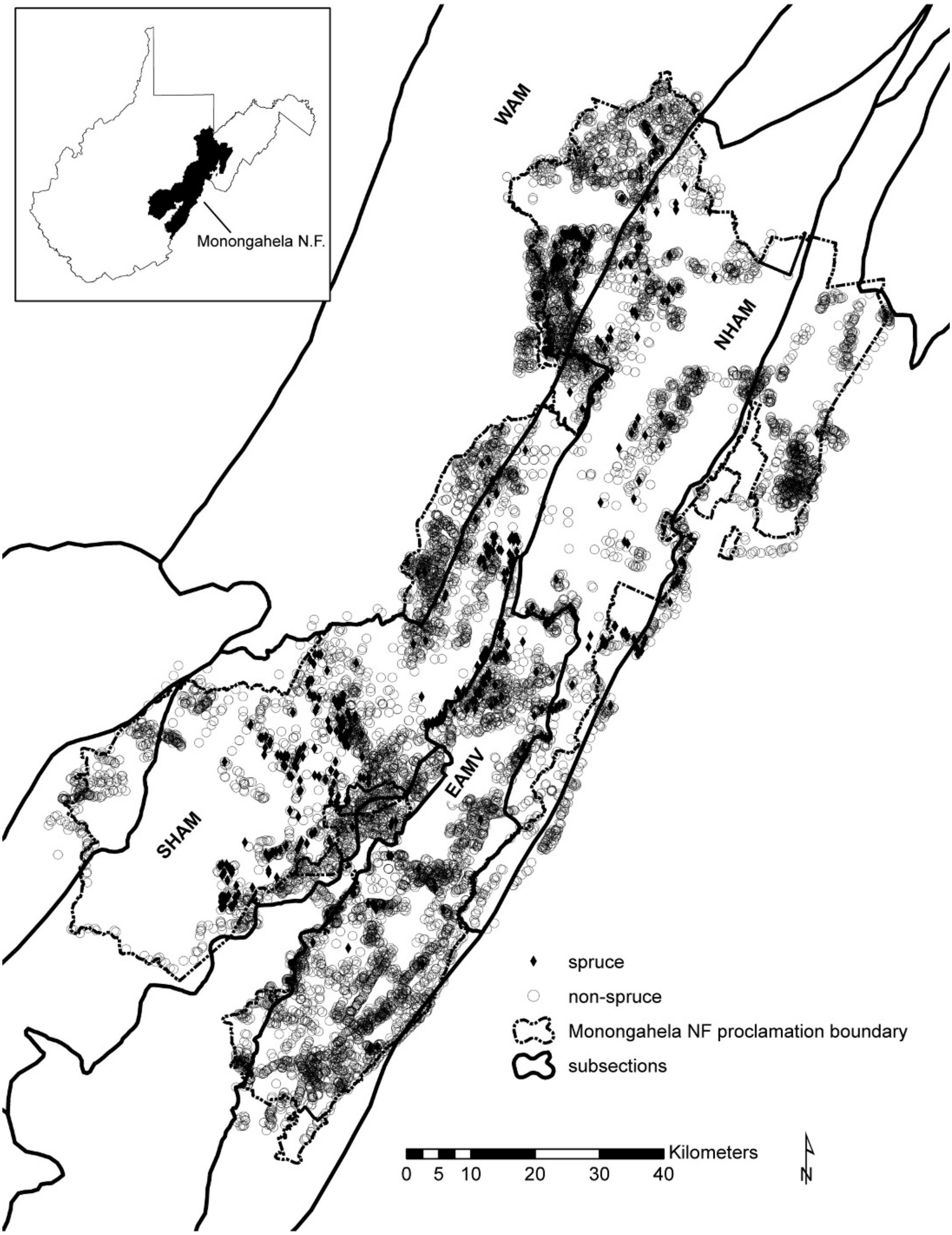

FIG. 1. Study area showing the locations of spruce and non-spruce occurrences relative to ecological subsections. Insert map shows the location of the Monongahela National Forest.

We used this witness tree database to describe the early forests in the uplands of West Virginia, comparing elevation, landform, aspect, and soil series of corners with spruce witness trees to those without spruce witness trees. The frequency of species co-occurring with spruce was also determined to better describe forest composition and a comparison made between sites with red spruce to sites without red spruce.

Table 1. Selected subsection climate and potential natural vegetation attributes (Cleland et al. 2007). Subsection abbreviations: EAMV = Eastern Allegheny Mountain and Valley, NHAM = Northern High Allegheny Mountain, SHAM = Southern High Allegheny Mountain, and WAM = Western Allegheny Mountain.

Subsection	Ave. annual max. temp. (°C)	Ave. annual min. temp. (°C)	Ave. jan. min. temp. (°C)	Ave. annual snowfall (cm)	Ave. annual precip. (cm)	Min. elev. (m)	Max. elev. (m)	Mean elev. (m)
EAMV	16.5	2.6	−8.8	120.5	111.0	523.3	1,461.8	824.5
NHAM	14.5	2.0	−9.4	263.5	128.2	511.5	1,454.5	1,020.2
SHAM	15.2	2.4	−9.0	224.5	138.1	446.8	1,478.6	1,043.7
WAM	15.1	3.0	−8.8	187.8	122.2	418.2	1,226.8	733.2

	Potential natural vegetation (%)				
	Appalachian oak forest	Mixed mesophytic forest	Northeastern spruce-fir forest	Northern hardwoods	Oak-hickory-pine forest
EAMV	58.9	0.0	0.2	40.9	0.0
NHAM	0.0	0.0	14.3	80.4	5.4
SHAM	4.5	23.3	21.1	51.2	0.0
WAM	26.6	38.0	0.0	35.3	0.1

Study Area. The MNF was established in east-central West Virginia in 1920 (Fig. 1). This unglaciated area straddles the faulted and folded mountains of the Ridge and Valley physiographic section and the uplifted and eroded Allegheny Mountains. Consequently, the topography is complex, resulting in a great variety of physical site features and plant communities. The Allegheny Front divides the two physiographic sections, creating a rain shadow effect to the east. Sedimentary rocks of Pennsylvanian, Mississippian, Devonian, Silurian, and Ordovician age underlie the study area. Lithology includes sandstones, shales, siltstones, coal, and limestone.

The two physiographic sections that cover the MNF can be further subdivided by ecological subsection to better capture the diversity of ecological conditions. The ecological subsections of the study area (771,715 ha) include: Eastern Allegheny Mountain and Valley (EAMV; 161,518 ha), Northern High Allegheny Mountain (NHAM; 215,591 ha), Southern High Allegheny Mountain (SHAM; 243,468 ha), and Western Allegheny Mountain (WAM; 151,138 ha); subsections are from Cleland et al. (2007) (Table 1). In general, the EAMV subsection is moderate in both moisture and temperature regimes. The WAM subsection is cool with moderate moisture. The SHAM and NHAM subsections are both wetter and cooler than the other subsections; however, NHAM has the lowest average temperatures whereas SHAM is more moderate.

Appalachian oak (*Quercus* L.) forest is considered the potential natural vegetation for the EAMV subsection. In contrast, a variable mixture of northern hardwood and spruce is the potential natural vegetation for the NHAM and SHAM subsections. The mixed mesophytic type comprises the potential natural vegetation for the WAM subsection (Table 1; Cleland et al. 2007).

The deeds used in this study date from 1752 to 1899, a period beginning with gradual European settlement and culminating with large-scale timber removal. The extractive logging boom (and associated fires and soil loss) that reshaped the original forest of West Virginia occurred between 1870 and 1920, reaching a peak in 1909 (Stephenson 1993). In the upland counties of the MNF, commercial timber was first removed from areas close to navigable rivers and streams starting about 1865 (Stephenson 1993). In the 1850s and 1870s, interstate rail lines were built in the region (Lewis 1998). Large-scale forest removal occurred after narrow-gauge railroads were built into the remote upland forests beginning around 1884 (Stephenson 1993), with the headwaters of the Greenbrier River in Pocahontas County reached by rail in 1903 (Lewis 1998).

Methods. The positional error associated with the corner points from the conversion of paper records to digital formats was estimated to be 21 m (Thomas-Van Gundy and Strager 2012). This distance was used to buffer the

Table 2. Total number of spruce (S) and non-spruce (NS) occurrences by ecological subsection and study area.

Location	S	NS	Total
EAMV	83	3,636	3,719
NHAM	83	1,461	1,544
SHAM	266	2,635	2,901
WAM	112	2,529	2,641
Study Area	544	10,261	10,805

corners when calculating values for environmental variables. Witness-tree locations were stratified by ecological subsection to best explain the possible ecological differences in spruce distribution. The analyses were made on 10,805 witness tree locations recording at least one tree of any species. Spruce was recorded on 544 corners across the study area and most corners had only one tree given as a witness tree (Table 2). Any witness tree given as spruce, red spruce, black spruce, or yew pine was tallied as spruce for this analysis. Surveys after 1899 were not included to avoid major European influences through actions such as land clearing, logging, and grazing. As these data were derived from historical records of point locations referenced in deeds, we assume the spruce witness trees are from forests representing a range of spruce dominance.

Elevation and aspect were derived in ArcMap (ESRI 2009) from a 1/9 arc second digital elevation model (DEM) of the study area (USGS 2003) that was resampled to 9 m to smooth artifacts present in the original cover. Elevation was calculated as an average for each point buffered by the positional error term (21 m). The GIS-derived aspect was transformed so that 0–22.5 degrees and 337.5–360 degrees both resulted in north aspect. Aspect was not averaged for each point; all calculated aspects found within the 21 m radius of the point were tallied.

Landform and soil series were extracted from existing MNF spatial datasets with corners buffered by the positional error term so that all landforms and soil series within the 21 m radius were tallied. Landform data were from the MNF ecological classification system and were assigned during soil surveys (USDA NRCS 2010). Landforms include: ridge/peak, bench/plateau, toe slope, side slope, cove, and floodplain/valley. Soil series were obtained from the MNF soils GIS layer based on 1:20,000 soil survey maps. Soil series were dropped from the analysis if they described less than 1% of the corners in the final database. Complexes of soils were summarized by the first soil series listed in the complex; for example Berks-Weikert soils were grouped with Berks soils for this analysis.

Descriptive statistics of the environmental characteristics were calculated for points with spruce and points without spruce. Two-sample *t*-tests were used to compare average elevation of points with and without spruce (SAS 2008; $\alpha = 0.05$). All other characteristics (landform, aspect, soil series, and frequency of co-occurring species) were individually summarized by points with or without spruce. Comparisons between frequency distributions of points with and without spruce were made using Kruskal-Wallis (K-W) tests (SAS 2008; $\alpha = 0.05$). In all comparisons, the null hypothesis was that there were no differences between the frequency distribution of points with or without spruce by site variable.

Indicator species analysis (ISA) with significance tested through Monte Carlo methods (4,999 permutations; $\alpha = 0.05$) was used on the tallies of categorical data by species in PC-ORD (McCune and Mefford 2006). Categorical variables (aspect, landform, elevation, soil series, and presence/absence of spruce) were used as grouping factors and each corner served as a plot for this analysis. Indicator species analysis combines the species abundance in a given group with the faithfulness of occurrence of a species to a group and has been used to describe site-species relationships (Phillips et al. 2003, Godefroid et al. 2007). The indicator value is the product of the proportional abundance of a species in a group relative to the abundance of that species in all groups and the mean proportion of sample units in each group that contain the species (McCune et al. 2002). If a species is a perfect indicator of a given group it should always be present in that group and exclusive to that group. Indicator species analysis calculates indicator values for each species and group with this perfect indicator as the reference (Dufrêne and Legendre 1997). Rare species or infrequent species/categorical variable combinations have little chance of being statistically significant indicators (McCune et al. 2002). Therefore, while the witness tree data may represent a range of spruce dominance, ISA is

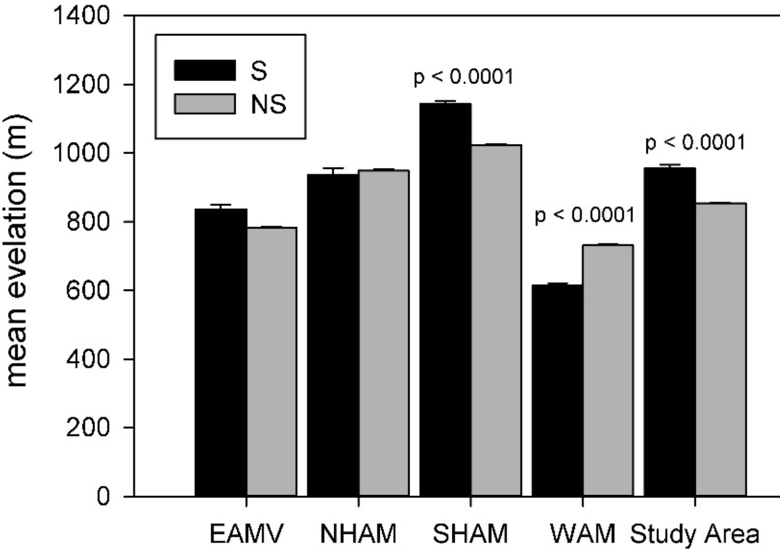

FIG. 2. Mean elevation at spruce (S) and non-spruce (NS) locations by subsection and study area; *P*-values are results of two-sample *t*-test.

not likely to find significant associations from chance occurrences of spruce.

Results. Across the entire study area and separately in the SHAM subsection, corners with spruce were higher in mean elevation than those without (Fig. 2). The WAM subsection stands out as the only subsection where spruce points were significantly lower in mean elevation than those without spruce (Fig. 2). The K-W test determined there were significant differences between landform frequencies of spruce and non-spruce points for the study area and all subsections (Fig. 3). In all subsections, over half of the spruce points were found on side slopes; however, side slope was also the most common landform of non-spruce points covering 62% of the study area (Fig. 3). Interestingly, in the WAM subsection, about 25% of the spruce points were on valley landforms and indicator species analysis determined that spruce points in this subsection were more likely to be on valley landforms that would be expected by chance. While toe slopes only represented 4% of spruce points (study area and EAMV subsection), indicator species analysis found that spruce points were significantly more likely on this landform in the EAMV subsection and study area than would occur by chance. Spruce were more likely to occur on bench landforms in the SHAM subsection than expected by chance, based on indicator species analysis.

Distributions of spruce points and non-spruce points by aspect were found to be significantly different for the study area as a whole and all subsections (Fig. 4). The aspect of spruce points varied by subsection with greater proportion of points on north aspects in the EAMV subsection (23%), northeast in the WAM subsection (22%), and northwest in the SHAM subsection (18%), and northeast and northwest in the NHAM subsection (18% each). Based on ISA, spruce in the WAM subsection were more likely to be found on northeast aspects, in the EAMV subsection spruce were more likely on north aspects, and more likely on northwest aspects in the SHAM subsection.

The distributions of spruce and non-spruce points by soil series were determined to be significantly different for the study area and the EAMV, NHAM, and SHAM subsections. Over half (60%) of the spruce points in the WAM subsection were on Gilpin soils compared to 40% of the non-spruce points (Table 3). In the SHAM subsection, as in the study area as a whole, the largest proportion of spruce points were found on Mandy soils (35%) compared to 12% of non-spruce points. In this subsection, 30% of the non-spruce points were found on Cateache soils. The two

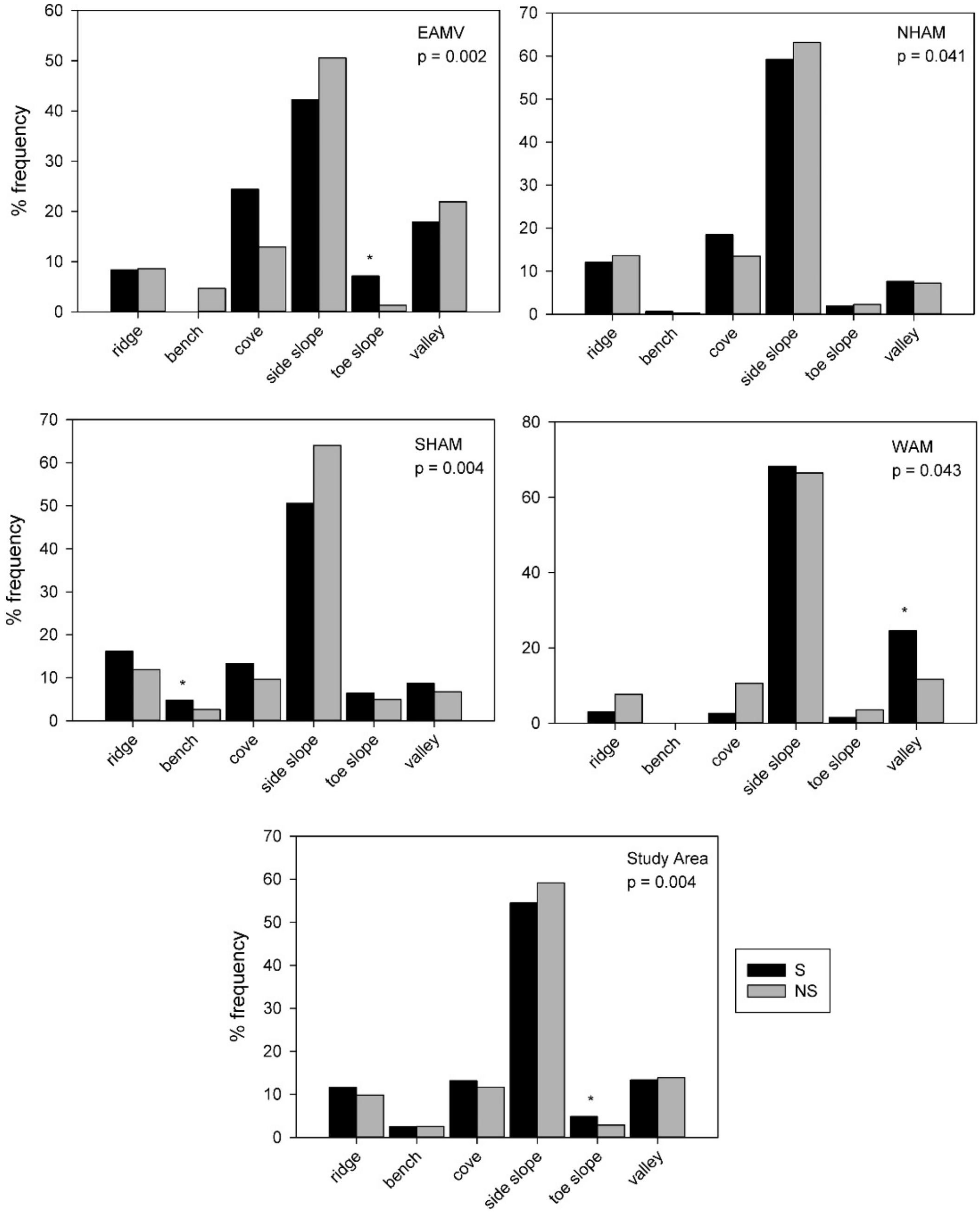

FIG. 3. Frequency of spruce (S) and non-spruce (NS) locations by landform and by subsection and study area; *P*-values are results of K-W test and * note significant results of indicator species analysis.

soil series, Mandy and Cateache, are associated geographically but differ in their soil temperature regimes with Mandy soils being frigid and Cateache mesic (USDA NRCS 1998). In the EAMV subsection, 34% of the spruce points were found on Berks soils as compared to 23% of the non-spruce points. Berks and Gilpin soils are geographically associated with Gilpin soils formed on nearly horizontal interbedded shale and siltstone in the Allegheny Plateau (USDA NRCS 2011). Indicator species analysis determined Mandy (study area),

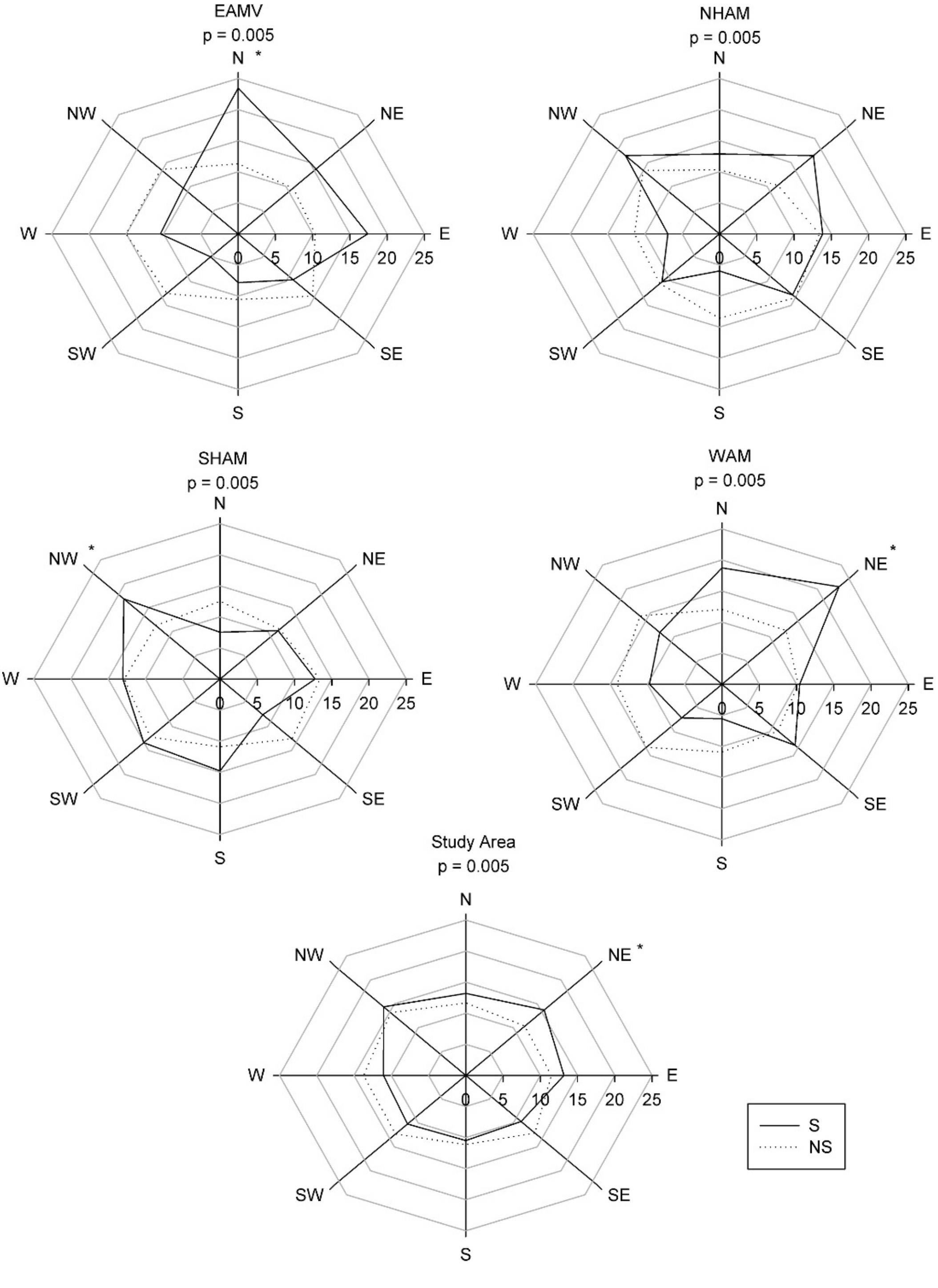

Fig. 4. Frequency of spruce (S) and non-spruce (NS) locations by aspect and by subsection and study area; *P*-values are results of K-W test and * note significant results of indicator species analysis. Axes are percentages of points by aspect.

Table 3. Frequency (percent) of spruce (S) and non-spruce (NS) corners by soil series across the study area and by subsection; * denotes a significant finding from indicator species analysis.

	Study Area		EAMV		NHAM		SHAM		WAM	
Soil Series	S	NS	S	NS	S	NS	S	NS	S	NS
Allegheny	0.7	1.4	1.2	3.4	0.0	0.1	0.0	0.0	2.5 *	0.4
Atkins	0.7	2.5	1.2	5.2	0.0	0.4	0.0	0.5	2.5	1.4
Belmont	1.6	5.4	1.2	0.8	7.2	15.2	0.8	8.8	0.0	3.8
Berks	9.0	14.5	34.8	23.0	4.0	7.2	1.3 *	0.3	9.6	20.1
Blackthorn	0.0	1.2	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0
Buchanan	3.4	1.5	0.0	0.0	2.4	0.4	6.3	4.4	0.0	1.4
Calvin	3.9	9.2	0.6	6.1	7.2	17.1	2.9	9.2	6.6	9.9
Cateache	10.1	11.1	0.6	0.5	2.4	17.6	19.6	30.0	0.0	4.5
Dekalb	8.4	8.0	1.2	2.1	20.8	20.9	6.9	7.6	9.6	10.9
Ernest	1.8	3.6	0.0	4.5	2.4	2.0	0.2	0.3	6.6	6.5
Gilpin	14.0	10.9	0.0	0.0	0.0	0.5	2.3	6.4	62.4	40.2
Laidig	0.0	0.4	0.0	0.0	0.0	0.2	0.0	1.5	0.0	0.0
Lily	0.5	0.7	0.6	1.4	0.0	0.2	0.8	0.3	0.0	0.0
Macove	2.5	4.7	14.3	12.0	0.8	0.4	0.0	0.0	0.0	0.0
Mandy	18.3 *	3.7	0.6	0.1	7.2	4.2	34.7	12.3	0.0	0.0
Meckesville	4.7	1.8	0.0	0.0	30.4	5.9	1.5	3.6	0.0	0.7
Potomac	3.8	3.9	11.8	8.0	3.2	2.9	2.7	1.5	0.0	0.0
Shouns	15.7	5.1	25.5 *	3.3	12.0	3.9	19.8	13.2	0.0	0.0
Weikert	1.0	10.3	6.2	26.4	0.0	0.8	0.0	0.0	0.1	0.0

Shouns (EAMV), Berks (SHAM), and Allegheny (WAM) soils to be significantly associated with spruce points.

Across the study area, 26 other species (or genera) occurred at least once with spruce at survey corners (Table 4). Black walnut (*Juglans nigra* L.), sycamore (*Plantanus occidentalis* L.), elm (*Ulmus* L.), black oak (*Quercus velutina* Lam.), hornbeam (*Carpinus caroliniana* Walter), and yellow pine species were not recorded at spruce points. The frequency of other species occurring at spruce corners differed by subsection and was found to be significantly different than the occurrences of species at non-spruce corners (Fig. 5). In the EAMV subsection, white oak (*Quercus alba* L.; 29%), maple (*Acer* L.; 14%), and basswood (*Tilia* L.; 17%) were the most frequent co-occurring species. Co-occurring species frequencies in the NHAM subsection differed from other subsections with hemlock (*Tsuga canadensis* (L.) Carrière; 23%) being the second-ranked species following American beech (*Fagus grandifolia* Ehrh.; 32.5%). The three most frequent co-occurring species in the SHAM subsection were American beech (31%), birch (26%) and sugar maple (*Acer saccharum* Marsh.; 11%). In the WAM subsection, birch (26%), white oak (21%), and American beech (12%) were the most frequent co-occurring species. Across the study area, American beech (24%), birch (19%), and maple (9%) were the most frequent associates of spruce.

When the presence of spruce is used as the grouping variable for indicator species analysis, American beech, birch, and hemlock are found to be associated with spruce across the study area. In one subsection (EAMV), basswood was found to be significantly associated with spruce. Species that could indicate the absence of spruce across the study area include pine (*Pinus* L.), hickory (*Carya* Nutt.), American chestnut, white oak, chestnut oak, red oak, and black oak. Surprisingly, two species found to be strongly associated with spruce in the study area as a whole were found to indicate the absence of spruce in one subsection; in the SHAM subsections, basswood and hemlock indicated an absence of spruce.

Discussion. Present spruce occurrence is strongly dependent on elevation (Nowacki et al. 2010) especially in West Virginia (Nowacki and Wendt 2010, Beane 2010). Elevation is a key gradient in mountainous regions reflecting many interrelated environmental factors, especially moisture and temperature. In the WAM subsection the average elevation at which we found spruce witness trees (620 m; minimum of 509 and maximum of 908 m) was slightly lower than a previous estimate of the minimum elevation for spruce at 700 m (Hopkins 1899). Spruce appears to compete best in cool and wet conditions (Nowacki and Wendt 2010), and was observed to occur in

Table 4. Frequency (percent) of other species at spruce (S) and non-spruce (NS) corners across the study area and by subsection.

Species	Common names used in deeds	ALL		EAMV		NHAM		SHAM		WAM	
		S	NS	S	NS	S	NS	S	NS	S	NS
Fagus grandifolia Ehrh.	Beech	24.2	9.7	2.7	1.2	32.5	19.4	31.0	17.9	11.5	9.2
Betula L.	Birch (no species given)	19.0	4.6	6.1	1.2	6.1	6.9	26.2	8.4	26.0	4.7
Acer L.	Maple (no species given)	9.2	6.0	15.0	6.7	7.4	6.3	8.4	5.2	7.7	5.8
Quercus alba L.	White oak	7.6	17.0	28.6	30.3	1.2	6.0	0	4.6	21.2	14.5
A. saccharum Marsh.	Sugartree, sugar maple, hard maple	7.1	11.8	2.7	5.1	1.8	18.9	11.2	20.5	3.8	8.8
Tilia americana L.	Basswood, yellow or white lin	7.1	4.9	11.6	3.4	16.6	6.3	4.0	7.5	0	3.3
Tsuga canadensis (L.) Carrière	Hemlock	5.3	1.4	0	0	23.3	4.9	1.3	2.5	1.9	0.3
Amelanchier Medik.	Serviceberry, service, sarvice	2.6	0.3	0.7	0.1	0	0.7	4.0	0.2	3.8	0.5
Castanea dentata (Marsh) Borkh.	Chestnut or American chestnut	2.5	5.6	7.5	5.3	0	3.7	1.1	4.2	5.8	9.7
Spruce-pine	Spruce-pine	2.4	2.0	3.1	0	1.2	2.2	4.2	1.0	0	1.1
Magnolia L.	Cucumber tree, magnolia, elkwood	1.6	1.5	0	0.1	0	2.7	1.5	1.8	6.7	3.2
Lirodendron tulipifera L.	Yellow-poplar, poplar, popple, tulip tree, tulip, tulip poplar	1.6	1.7	5.4	1.0	1.8	1.2	0.4	0.8	1.0	4.8
Fraxinus L.	Ash (all species)	1.6	2.1	0	1.0	0.6	2.6	2.9	3.0	0	2.8
Q. coccinea Münchh.	Scarlet oak, span oak, Spanish oak	1.3	1.8	2.7	0.8	1.8	2.6	0.4	0.9	1.9	4.6
Pinus strobus L.	White pine	1.3	1.3	4.8	3.2	0	0	0	0	3.8	0.2
Aesculus L.	Buckeye (all species)	0.9	0.2	0	0.2	4.9	0	0	0.2	0	0.2
Carya Nutt.	Hickory (all species)	0.8	5.1	4.1	7.7	0	1.5	0	2.6	1.0	5.8
Nyssa sylvatica Marsh.	Blackgum, tupelo, sour gum	0.7	1.1	0	1.2	0.6	0.5	0.4	0.6	2.9	1.9
Q. rubra L.	Red oak	0.7	3.7	3.4	2.8	0	3.3	0.2	4.3	0	2.5
Prunus serotina Ehrh.	Black cherry, wild cherry	0.7	1.6	0	0.8	0	2.2	1.3	3.3	0	0.5
Ostrya virginiana Scop.	Hophornbeam, hopwood	0.6	1.3	0	1.1	0	2.0	1.1	1.8	0	0.5
Q. prinus L.	Chestnut oak, rock oak	0.3	3.9	2	4.9	0	1.9	0	0.5	0	8.0
Juglans cinerea L.	Butternut, white walnut	0.3	0.6	2	0.4	0	0.4	0	1.0	0	0.7
Robinia pseudoacacia L	Locust, black locust	0.2	0.9	0	0.9	0	0.6	0.4	1.1	0	0.8
Pinus L.	Pine (no species given)	0.1	5.0	0.7	9.3	0	0.9	0	3.8	0	0.6
Cornus florida L.	Dogwood	0.1	1.6	0	2.8	0	0.6	0	0.2	1.0	1.6

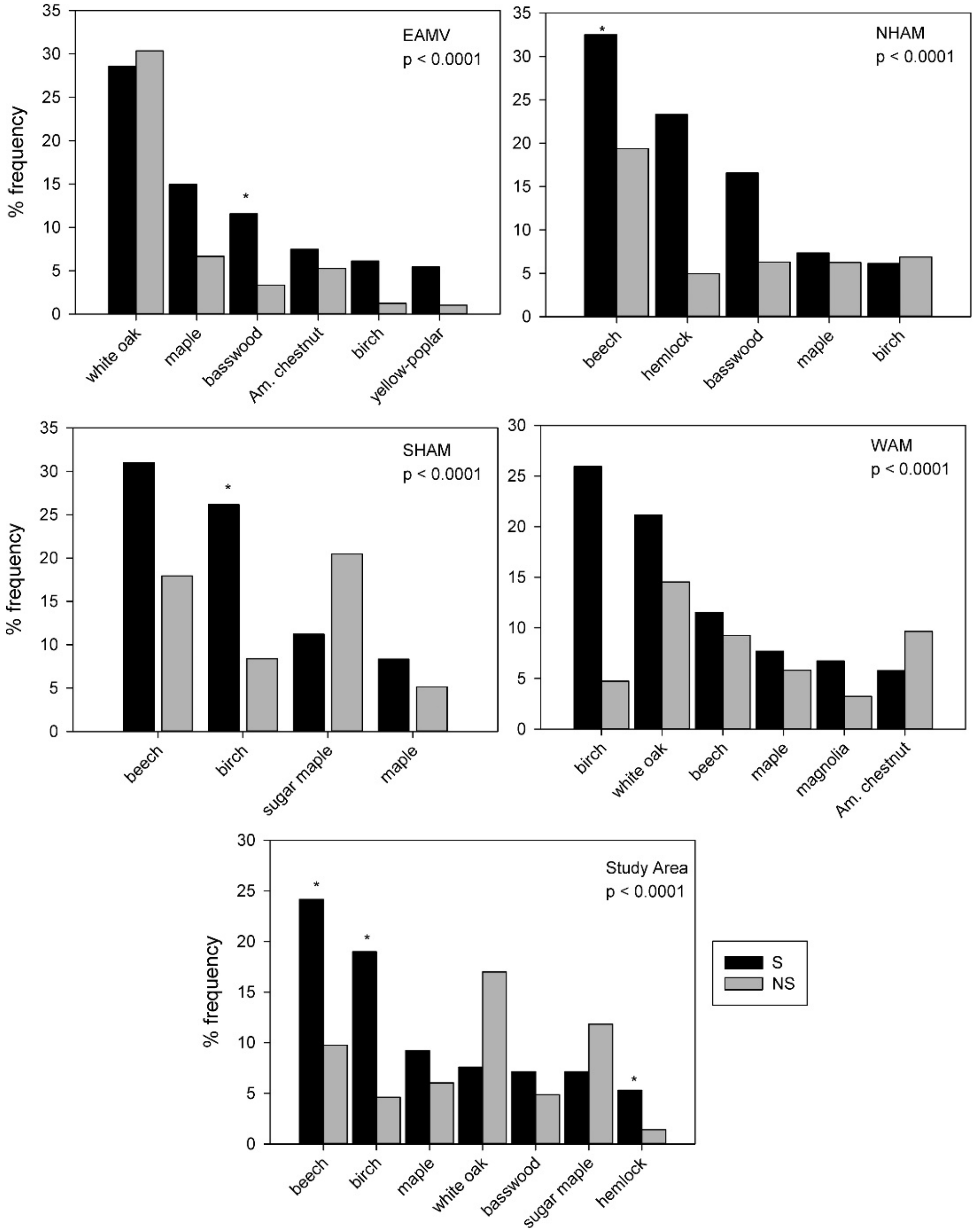

FIG. 5. Frequency of species other than spruce at spruce (S) and non-spruce (NS) locations by subsection and study area; *p*-values are results of K-W tests. Only species with 5% or greater frequency on spruce locations are shown, a complete list of species and frequencies is found in Table 3.

valley floors in presettlement forests (Allard and Leonard 1952). Indicator species analysis determined that spruce trees in the WAM subsection were associated with valley landforms, suggesting that wet and cool conditions favorable to the species occurred at lower elevations in this subsection.

Aspect was not found to be a significant predictor of spruce occurrence in studies of current forests (Menzel et al. 2006, Hayes et al.

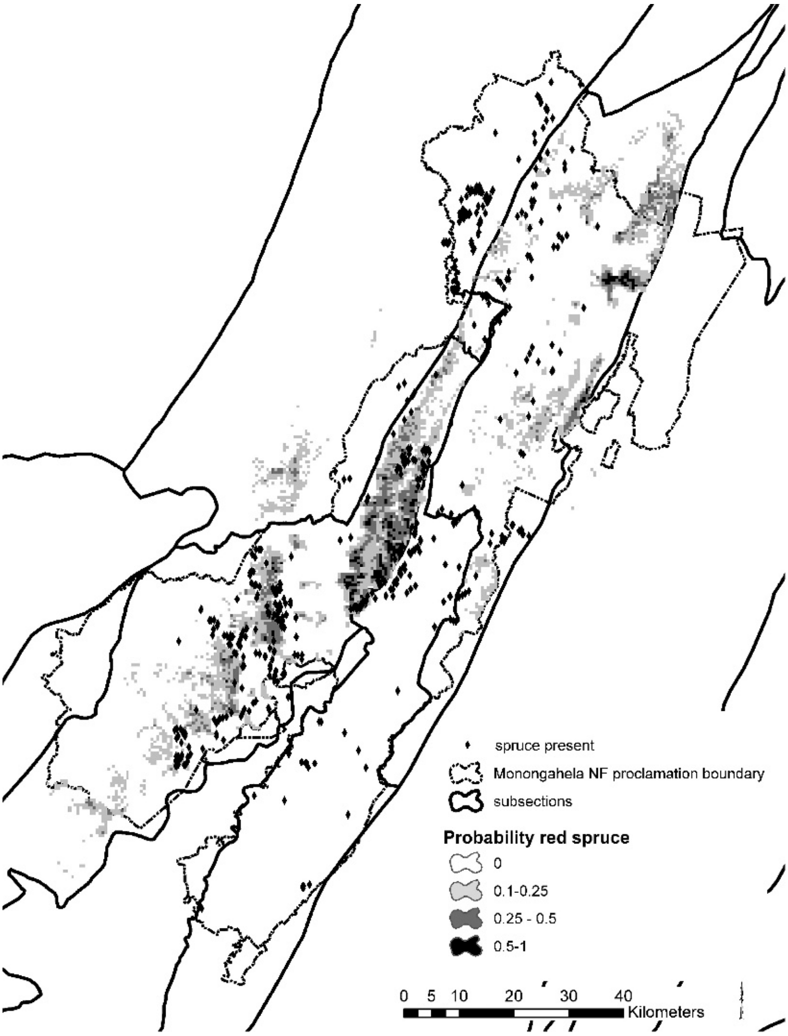

FIG. 6. Locations of spruce occurrences and a calculated probability of red spruce occurrence (Nowacki and Wendt 2010).

2006, Beane 2010, Nowacki and Wendt 2010). However, our indicator species analysis determined that, historically, spruce was more likely to be found on northerly aspects in three of the ecological subsections and across the study area (Fig. 4). It makes ecological sense that spruce would be more prevalent on north-facing slopes due to their shaded (cool) and mesic tendencies.

Species co-occurring with spruce differed among subsections consistent with the inherent environmental differences between subsections suggesting that the witness trees represent mixed spruce-hardwood forests. The drier EAMV subsection (Table 1) has a greater frequency of white oak (29%) compared to the more mesic SHAM (0%) or NHAM (1%) subsections. In the NHAM subsection, 23% of the co-occurring witness trees were hemlock, whereas the frequency was much less in the other subsections and only 5% across the study area. Studies of contemporary forests have also determined spruce to be associated with yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), hemlock, and black cherry (*Prunus serotina* Ehrh.) (Stephenson and Clovis 1983, Nowacki et al. 2010), but not with oaks (Beane 2010). However, these studies may have excluded areas that historically supported spruce because such areas currently lack the species. A previous analysis of the entire witness-tree database concluded that birch witness trees were most likely yellow birch - based on their association with high elevations and Mandy soils (Thomas-Van Gundy and Strager 2012) - a finding echoed in current close relations between yellow birch and spruce in the Central Appalachians (Nowacki et al. 2010).

The existence of a water-restricting layer in the soil (fragipan) has been considered important in current spruce forests (Nowacki and Wendt 2010). Two soils associated with spruce witness trees in this study, Meckesville soils and soils in the Mandy soil series, can contain fragipans (USDA NRCS 2011). These finding are consistent with models of existing spruce forests in the study area (Beane 2010, Nowacki and Wendt 2010) with Trussel-Mandy-Snowdog, Shouns-Cateache-Belmont, and Dekalb-Buchanan soils describing 75% of the current spruce locations studied (Beane 2010). However, the location of the current spruce-dominated forests on wetter sites may be a result of past land use, as hardwood competition after industrial logging would have been less on those sites (Nowacki and Wendt 2010).

Abrams and McCay (1996) found that 2.3% of presettlement forests in the Allegheny Mountains and 0.1% of forests in the Ridge and Valley sections of the study area were comprised of red spruce. Very few spruce witness trees were used in the 1996 study, complicating comparisons between this study and the current findings. Based on the current study, 5.0% of the corners recorded spruce across the study area. There are many differences between the 1996 study and the current study including the current study involving a larger study area, more deeds, and spanning different, but overlapping, timeframes.

Although it is difficult to determine if these spruce witness trees represent pure or mixed forests, the analysis of species occurring with spruce at the same deed corner would suggest that these data represent mixed forests. Across the study area, 26 other species were found with spruce with any frequency but only two at 10% or greater frequency (Table 4). With the exception of white oak in the EAMV and WAM subsections, the other species with greater than 10% frequency on any subsection (American beech, birch, maple, sugar maple, basswood, and hemlock) are all known associates in a spruce-northern hardwood forest (Eyre 1980). Restoration goals for spruce forests on the MNF pertain to spruce-dominated forests, not just pure spruce forests (USDA 2006), and so information from this witness tree database can inform these efforts regardless of the uncertainties of spruce dominance.

A comparison of the spruce witness tree locations to a calculated probability of red spruce occurrence (Nowacki and Wendt 2010) shows areas of general agreement and some discrepancies (Fig. 6). The WAM and EAMV subsections stand out as areas where red spruce had a low probability of occurrence, yet spruce were documented as witness trees. The predictive map, based on edaphic and climate data, shows some likelihood of spruce occurrence in the southern end of the WAM subsection at higher elevations. That area was not covered by the witness tree database, being just outside the MNF proclamation boundary. Further north in the WAM subsection the predictive model does overlap with the witness tree database, and while spruce witness trees were present, the Nowacki and Wendt (2010) model determined no probability of spruce occurrence. The predictive model boundary generally follows the subsection boundary in the EAMV subsection, and the lack of predicted spruce occurrence is likely due to an elevation cutoff here as well. However, interpolation between spruce witness tree locations shows low probability of spruce presence in the two subsections with about 11,300 ha of 5–40% probability of occurrence in the WAM subsection and 17,000 ha in the EAMV subsection (Thomas-Van Gundy and Strager 2012). Thus, witness tree data coupled with predictive maps can validate and further improve restoration determinations of spruce forests.

In the EAMV subsection, suitable sites for spruce restoration may be found on toe slopes, northern aspects, or Shouns soils. No significant difference in mean elevation between spruce and non-spruce sites was found in the NHAM subsection, suggesting that elevation should not be a limiting factor for determining restoration sites in this subsection. Although no one soil series was found to be associated with spruce sites in the NHAM subsection, Meckesville soils supported spruce witness trees in greater number than non-spruce witness trees. Spruce witness trees occurring in the SHAM subsection exhibited more similarities with current red spruce distribution. In this subsection, mean elevation of spruce points was significantly higher than non-spruce points and spruce were associated with birch and Berks soils. In contrast, spruce witness trees in the WAM subsection were found at lower mean elevations, on valley landforms, Allegheny soils, and northeast aspects suggesting very different locations for spruce restoration. Based on the locations of spruce witness trees in this historical database, restoration efforts should not be limited to the current extent of red spruce, such as high elevation ridge tops.

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