

Ghosts of the forest: Mapping pedomemory to guide forest restoration



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ABSTRACT

Soil morphology can provide insight into how ecosystems change following periods of extensive disturbance. Soils properties can often be linked to historic environmental influences (e.g., vegetation or climate) to provide a record of pedomemory. Identification and mapping of soil pedomemory properties show promise in providing context for ecological restoration. We have developed a novel use of digital soil mapping of spodic morphology to estimate historical forest composition in the high-elevation forests of the Central Appalachians. This region was extensively disturbed by clear-cut harvests and related fires during the 1880s–1930s. Hardwood forest species recovered much better than local conifers and generally encroached into historic populations of red spruce (*Picea rubens*) and eastern hemlock (*Tsuga canadensis*). Spodic soil morphology, which is often associated with subalpine and boreal conifer forests, was mapped using a random forest probability model and showed correspondence to red spruce – eastern hemlock distribution, as derived from local historic property deed witness tree records from 1752 to 1899. These data and resulting models indicate a greater spatial extent of spodic soil properties than documented in previous soil maps, which is more consistent with general theories of much more extensive historic spruce populations. The resulting maps and models provide guidance for field scale restoration planning for historically disturbed spruce–hemlock forests. Our results suggest that historic Euro-American disturbance probably induced conifer-to-hardwood state transitions at mid to high elevation coniferous ecological sites within the Appalachians. Where transitions have occurred, there appears to have been dramatic losses in forest floor thickness (O-horizons) and associated soil organic carbon stocks into atmospheric carbon pools. Spatial modeling of similar pedomemory properties and other soil-ecology linkages is likely to be a powerful tool to guide restoration in other regions as well.

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1. Introduction

1.1. Soil pathways and pedomemory

Soil properties can help reveal the history of interactions between abiotic and biotic drivers at the Earth's surface. In soil science, this has been conceptualized as a state factor model where the state or properties of a soil are a result of interactions between climate, organisms, relief, and parent material over time (clorpt) (Dokuchaev, 1999; Jenny, 1941). The state factor model evolved to an ecosystem level model where soils and organisms have some parallel drivers, but also interact strongly (Amundson and Jenny, 1997; Jenny, 1961, 1980). Eq. (1) reformats Jenny (1941) 'clorpt' model into an ecological equation where different groups of the original soil forming factors interact

over time to result in a set of ecosystem properties (including soil) at a given point in time.

$$l, s, v, a = f(L_0, P_x, t) \quad (1)$$

Ecological factorial; Jenny (1961).

The dependent factors in this case include ecosystem properties (l), soil properties (s), vegetation (v), and animals (a). The related state factors in an ecosystem based approach include the initial state (L_0) and external potentials (P_x), and time (t). Initial state L_0 includes the parent material (bedrock or substrate), initial relief, and water table. Climate and organism changes are grouped as the P_x variable, which represent the primary energy sources (sun), receptors (plants), and catalysts (e.g., water) that drive processes (Jenny, 1961). Amundson and Jenny (1991, 1997) have introduced these conceptual models into ecological sciences, with humans included in the factorial equation. In an ecosystem, soils bear the imprint and help record the history of organisms – including humans – as well as the climate. For conceptual

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and measurement purposes, we define an ecosystem as the living organisms and physical environment of a defined unit space or a plot (e.g., 20 × 20 m) that we can sample in the field.

Climatic and biological factors drive processes in soils that involve additions, removals, translocations, and transformations (Simonson, 1959) of materials in the soil column that have associated energies (Nikiforoff, 1959; Runge, 1973). When environmental drivers remain relatively constant over a period of time they can direct a soil down a developmental pathway toward expressions of specific horization (Johnson and Watson-Stegner, 1987). Changes in climate and/or organisms can alter the balance of processes and thus the pathway of a soil. At any one time, many processes are occurring in a soil, which can create complicated superimposed distributions of soil properties within a soil profile (Burrough, 1983).

The properties observed in soils reflect a record of information, often called soil memory or pedomemory, where the specific patterns of reorganization and transformation of the original soil parent material into new physical and chemical distributions in the soil profile can often be attributed to how historic climate and vegetation promote soil processes that result in a specific morphology (Hole, 1975; Lin, 2011; Targulian and Goryachkin, 2004). Related studies have linked mottling, iron chemistry, and other morphology to historic soil–water–landscape models (Coventry et al., 1983; Coventry and Williams, 1984; Fritsch and Fitzpatrick, 1994; Schwertmann, 1988). Others have found that vegetation communities interact with the soil over time to create soil property signatures recorded in the pedomemory useful in determining a site history (Hole, 1975; Phillips and Marion, 2004; Willis et al., 1997). Thus, a soil property like spodic materials can potentially provide a time–space record that can help decipher historic ecosystem vegetative reference conditions, which are an accepted basis for ecological restoration to a certain target community type and condition (Higgs et al., 2014; SER, 2004; <http://www.ser.org/resources/resources-detail-view/ser-international-primer-on-ecological-restoration>). Linking soil types with historic reference communities has become the basis for land management frameworks such as ecological site descriptions (ESD) (Caudle et al., 2013; USDA-NRCS, 2014). We aim to show how mapping key pedomemory properties linked to vegetative communities can inform restoration at a field ecosystem scale. We demonstrate this using an example along the ecologically important transition between northern hardwood and spruce–hemlock forest types in the Central Appalachian mountains of the eastern US (Byers et al., 2010).

For distinguishing the historic transition between northern hardwood and spruce–hemlock, we chose the podzolization pathway (Lundström et al., 2000a,b; Sauer et al., 2007; Schaeztl and Harris, 2011) as our pedomemory indicator because of its association with similar moist conifer forest and heathland species composition globally (Hole, 1975; Miles, 1985; Willis et al., 1997; Lundström et al., 2000a; Sauer et al., 2007). In a typical cool, moist conifer site where Spodosols form as a result of podzolization, the soil morphology generally is a sequence of Oi–Oe–Oa surface horizons forming a mor forest floor, then a leached E horizon, and a sequence of Bh–Bhs–Bs–BC subsurface horizons (Fig. 1) (Soil Survey Staff, 1999; Soil Survey Staff, 2010). The podzolization pathway includes multiple soil processes that promote aluminum, iron, and organic matter mobilization and translocation to deeper soil depths in acidic, permeable parent materials. Thick surface O horizons also frequently form at the soil surface in these typically moist conifer systems (Hix and Barnes, 1984; Lietzke and McGuire, 1987; Lundström et al., 2000a). Leaching is usually associated with soluble organic acids from the forest floor and actively mining ectomycorrhizal communities causing mineral weathering and the ultimate transport of aluminum, iron, and organic matter from near surface soil horizons (O, A, E) into subsurface (B) soil horizons (Blum et al., 2002; Giesler et al., 2000; Hoffland et al., 2004; Jongmans et al., 1997; Lundström et al., 2000b; Schaeztl and Harris, 2011; Schöll et al., 2008; van Breemen et al., 2000).

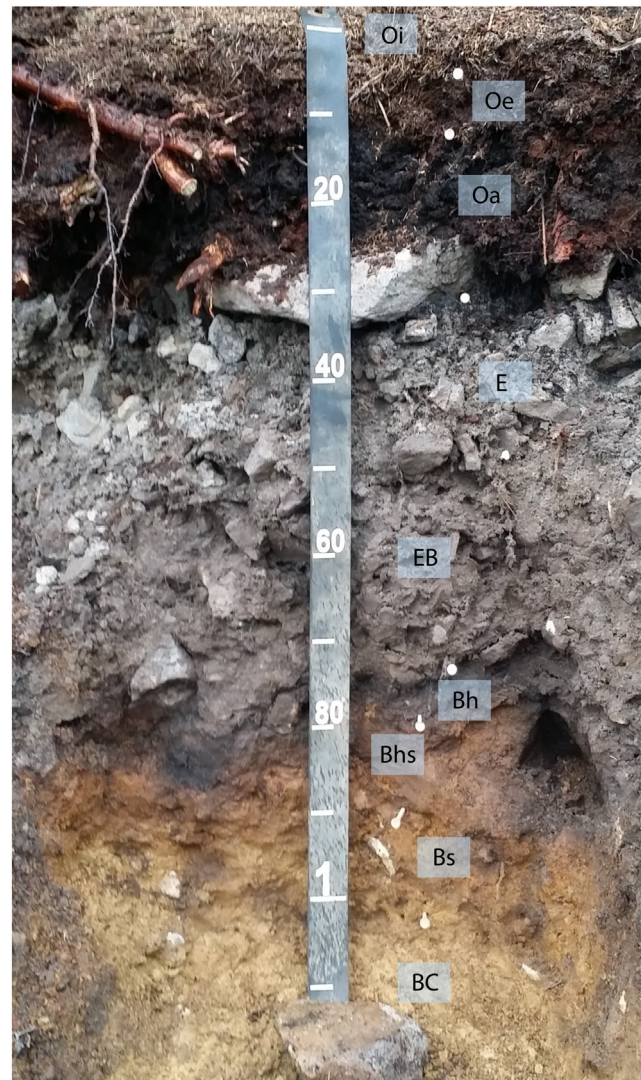


Fig. 1. Well expressed podzol soil morphology in a red spruce forest in WV.

Much of the organic carbon distribution in Spodosols can be lost in 30–100 years just by converting cool, moist acidic conifer forest stands to differing species compositions (prairie or hardwood) that favor more decomposition (Barrett and Schaeztl, 1998; Hix and Barnes, 1984; Hole, 1975; Miles, 1985). The most pronounced losses in organic carbon occur in the forest floor O horizons, which generally get thinner in conversions. Conversely, studies have also demonstrated that conversion from mesic hardwood forests (mostly *Quercus* spp., *Betula* spp., and *Fagus* spp.) to Norway spruce (*Picea abies*) and/or scots pine (*Pinus sylvestris*) initiates O horizon buildup and podzolization within a century (Herbauts and Buyl, 1981; Miles, 1985; Ranger and Nys, 1994; Sohet et al., 1988). Common garden experiments studying replanted monoculture plots of various tree species have also documented tree species gradients of influence on soil organic matter accumulation and acidity. On the two extremes, *Acer* spp. and *Tilia* spp. promote increased base cation activity which favors heterotrophic organic matter decomposition, whereas *Pinus* spp. and *Larix decidua* enhance acidic Al and Fe activity which limit decomposition of soil organic matter (Hobbie et al., 2007). Garden experiments also showed higher tree litter calcium content appeared to increase pH, decomposition, and earthworm activity that resulted in less forest floor mass (Reich et al., 2005; Hobbie et al., 2006). Hobbie et al. (2006) also recorded that plots with spruce and fir species had lower mean annual soil temperatures and less litter decomposition. Although general differences in litter

chemistry exist between angiosperms (basic) and gymnosperms (acidic), these studies showed that there is significant variation within these tree groups. Another recent common garden study in New York documented a similar influence of worms under northern red oak (*Quercus rubra*) and sugar maple (*Acer saccharum*), but not under Norway spruce, which had a thicker forest floor (Melvin and Goodale, 2013). Although Ca^{2+} content was similar under all three species, pH was lower under the spruce, suggesting that base cation activity might not be the only factor to examine. Other studies of tree species interactions with soil have recorded similar trends (Finzi et al., 1998; Van Breemen and Finzi, 1998). Overall, these studies tell a story where heterotrophic forest litter decomposition and O horizon accumulation are intricately linked to dominant tree species at a site.

Autotrophic mycorrhizal partnerships are another important consideration in understanding carbon and nutrient cycling in soils (Högberg and Read, 2006). Studies have demonstrated intensive ectomycorrhizal (ECM) colonization of E horizons that appear to be a significant nutrient acquisition adaptation strategy of conifers in acidic Al-dominated soil environments, thereby overcoming conditions that might otherwise be toxic (Blum et al., 2002; Giesler et al., 2000; Hoffland et al., 2004; Högberg and Read, 2006; Jongmans et al., 1997; Lundström et al., 2000b; van Breemen et al., 2000). Giesler et al. (2000) were able to show that the expansion of mineral-boring ECM hyphae looking for other nutrients is a likely mechanism for Al, Fe and Si transport to, and subsequent flux out of, O horizons. The buildup of autotrophic root hypha in the forest floor and associated host carbon allocation seems to be much more dominant processes than the classic heterotrophic model of litter and fine root decomposition and respiration in acid conifer systems (Högberg and Read, 2006). The development of deep O horizons under acidic conifer must, by definition, mean that heterotrophic communities are either suppressed or very inefficient in cycling carbon in these systems, which is also consistent with the results of garden studies (Reich et al., 2005; Hobbie et al., 2006, 2007).

Red spruce is one of the most acidophilic conifers, producing nutrient-poor litter (especially low in Ca^{2+}) relative to other North American trees (compare from: Berg and McLaugherty, 2008; Côté and Fyles, 1994; Friedland et al., 1988; Rustad and Fernandez, 1998). This implies that red spruce should promote podzolization and O horizon accumulation (Herbauts and Buyl, 1981; Lundström et al., 2000a; Miles, 1985; Ranger and Nys, 1994; Sauer et al., 2007; Sohet et al., 1988). Conversely, we expect that where spruce was converted to base-promoting hardwoods, like red maple (*Acer rubrum*), black cherry (*Prunus serotina*), and American beech (*Fagus grandifolia*), organic material loss has probably occurred from O and B horizons (Hix and Barnes, 1984; Miles, 1985; Hole, 1975). O horizon loss was probably initially exacerbated by the large-scale fires documented in these parts of West Virginia (WV) after mass clearcutting between 1860 and 1920 (Clarkson, 1964; Hopkins, 1899; Pauley, 2008). Well-developed Spodosols often take 1000–6000 years to form in areas similar to red spruce ecosystems (Lundström et al., 2000a; Schaeztl and Harris, 2011). Loss of Spodosol morphology is not as well documented, but was reported to disappear from a watershed in Hungary in 1000 years after a change in climate triggered a sequence of fires that likely converted forest stands from conifer to hardwood (Willis et al., 1997). However, the Fe and Al sesquioxide accumulations (spodic soil materials in US soil taxonomy; Soil Survey Staff, 1999) in the subsurface soil should still be observable as these are more stable and persistent in soils within the 150–250 year timeframe in this study (Barrett and Schaeztl, 1998; Lundström et al., 2000b; Parfitt, 2009). Indeed, Al-protomogolite, the major diagnostic sesquioxide solid compound in Spodosols, is relatively stable in soils for many millennia when soils maintain a pH greater than four (Parfitt, 2009). We hypothesized that Fe and especially Al sesquioxide accumulation found in Bhs and Bs (spodic) soil horizons should be good pedomemory evidence for pre-Euro-American spruce–hemlock influence.

Recent work related to ESD development in the Monongahela National Forest (MNF) in WV for the purpose of linking management strategies to pre-settlement vegetation and site potential has suggested that spodic soil properties are linked to past red spruce and eastern hemlock distributions (Nowacki and Wendt, 2010; Teets, 2013). In the most impacted sites where O horizons were probably lost and E horizons were likely transformed or lost due to hardwood conversion, erosion, and/or fires, we think remnant Bs horizons could be a good indicator of past spruce influence. Although we think historic podzolization of these areas was due in large part to the red spruce acidic foliar chemistry, shallow root distribution, and acid producing mycorrhizal activity (Blum et al., 2002; Glenn et al., 1991), there are also climatic parallels between red spruce and eastern hemlock physiological requirements and podzolization. Both require cold and moist environments and are favored by longer winter snowpacks and thus should follow analogous topographic patterns (Lietzke and McGuire, 1987; Schaeztl and Isard, 1996; Nowacki and Wendt, 2010; Nowacki et al., 2010; Stanley and Ciolkosz, 1981). Published modern soil surveys for counties of the MNF only delineate Spodosols on the highest sandstone ridges where red spruce has more successfully regenerated from past disturbance (Delp, 1998; Flegel, 1998; USDA-SCS and USDA-FS, 1982), but not down into siltstone and shale parent materials at slightly lower elevations that are still within the local range of red spruce based on current inventories and related models (Beane et al., 2013; Byers et al., 2010; Nowacki and Wendt, 2010) as well as historic witness tree species related species distribution models from historic county property boundary records (Thomas-Van Gundy et al., 2012). However, an older soil survey (Williams and Fridley, 1931) supports existence of a much larger area of podzol soils, which we believe corresponds to the more extensive historical distribution of red spruce forest communities prior to the regional harvest and fire disturbance of the late 19th and early 20th centuries. The vast majority of the harvest and fires occurred between 1880 and 1930, but site specific dates are hard to find. It is thought that very few places were not harvested in this period, and that fires also affected the vast majority of the landscape, but historic records are somewhat general in descriptions (Hopkins, 1899; Clarkson, 1964; Pauley, 2008).

1.2. Importance of red spruce forests in the Central Appalachians

Vast forests of red spruce (*P. rubens*), either singly or in association with northern hardwoods, once covered the higher elevations of the Central Appalachians (Hopkins, 1899). This assemblage is thought to have spanned the last 4–5 millenia (Watts, 1979), and strong associations developed between these forests and various animals, with sensitive species becoming somewhat reliant on red spruce habitat, such as the Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*) and Cheat Mountain salamander (*Plethodon nettingi*) (Dillard et al., 2008a, b; Menzel et al., 2004, 2006a,b; Pauley, 2008). Wind and ice storms were the principal disturbance agents in presettlement times as the prevailing cool, moist climate greatly retarded fire (Rentch et al., 2010). As such, the natural disturbance regime was probably driven by periodic light-to-moderate severity storms rather than by catastrophic blowdowns and old-growth conditions were abundant. The Euro-American disturbances of the late-1800s to early 1900s were in stark contrast to this naturally low-disturbance environment. As a valuable timber species, red spruce was quickly liquidated by industrial clear-cut logging once railroad technologies afforded access to mountainous areas (Clarkson, 1964; Lewis, 1998; Nowacki and Wendt, 2010). Thereafter, uncontrolled wildfires burned through the remaining slash, largely consuming red spruce regeneration in the process. The rapidity and voracity of these disturbances completely devastated red spruce, causing significant contraction to its population and range.

Due to its ecological and economic importance, red spruce restoration has received much attention in the Central Appalachian region (e.g., Central Appalachian Spruce Restoration Initiative; <http://www.>

restoredspruce.org/). Unfortunately, efforts to restore red spruce are thwarted by the fact that its former range is so poorly documented at the field scale—although recent attempts through modeling (Beane et al., 2013; Byers et al., 2010; Nowacki and Wendt, 2010) and witness-tree analyses (Thomas-Van Gundy et al., 2012) have provided greater clarity on its original distribution.

In West Virginia, historical accounts indicate that the current extent (~20,000 ha) of alpine red spruce forest communities is greatly reduced from estimates prior to railroad era disturbance (~200,000 ha) (Hopkins, 1899; Pauley, 2008; Pielke, 1981; Nowacki and Wendt, 2010). Local studies, along with regional analysis of red spruce distribution (Nowacki et al., 2010), show that the main restriction on red spruce is warmer temperatures (with elevation as a surrogate) and lower precipitation. However, recent work in compiling and analyzing witness-tree databases from the MNF indicates a lower minimum elevation historically (lowest recorded red spruce at 509 m) than previous models, and more specificity to topographic controls in respect to slope steepness, slope position, slope aspect, and landforms (Thomas-Van Gundy et al., 2012). These subtleties in the pre-settlement distribution of red spruce might indicate historic affinity for topographically-driven cool and moist microclimates that included the highest ridgelines, cooler aspects not in rain shadows, and narrow valleys that foster cold air drainage and foggy inversions.

Human disturbance and pollution have drastically impacted red spruce populations, but climate change and warming temperatures may have also affected populations — and these phenomena are hard to distinguish (Hamburg and Cogbill, 1988). Theoretically, global warming will drive boreal conifer ecosystem species like red spruce higher in elevation and further north, putting large pools of soil organic carbon at risk for further atmospheric release (Lal, 2005; Tarnocai et al., 2009). It is also hard to account for climate-vegetation feedbacks as well, and restoring to more historic communities could mitigate these potential feedbacks. Studies have shown that convectively driven precipitation patterns and radiative dynamics are influenced by changing vegetation type and structure which is likely to mean warmer and drier soil conditions for former spruce sites (Pielke, 1981, 2001; Pielke et al., 2002). Other concerns about acid deposition on red spruce health have been studied (Johnson, 1983; Hornbeck and Smith, 1985; Adams and Eagar, 1992), but might be difficult to discern from the impact of historic disturbance and climate change (Hamburg and Cogbill, 1988). Indeed, red spruce is projected by different climate change scenarios to disappear from West Virginia by the end of the century (Butler et al., in press; Byers et al., 2010; Iverson et al., 2008; Prasad et al., 2007). However, there are signs that red spruce is recovering from historic disturbance and could be further restored despite climate change (Nowacki et al., 2010; Rentch et al., 2007; Rentch et al., 2010; Rollins et al., 2010). At this time, its future remains uncertain, which has prompted this effort to try to better understand its historic distribution and dynamics.

1.3. Digital soil mapping of podzolization

Digital soil mapping (DSM) of soil properties often utilizes digital elevation model (DEM) derivatives, remotely sensed imagery, and climate surfaces as predictive soil forming factor surrogates using geographic information systems (GIS) and computer-based statistical modeling (Grunwald, 2009; Grunwald et al., 2011; McBratney et al., 2003; Scull et al., 2003). Although many DSM studies are aimed at predicting certain soil classes or soil properties at specified depths (e.g., Behrens et al., 2014; Yang et al., 2011), the same general structure can be applied to predicting a soil pathway such as podzolization because the active soil formation factors being represented by topography and imagery (climate and organisms) drive the processes that produce spodic soil properties. We postulated that an effective spatial model of spodic morphology should spatially correlate to the distribution of red spruce and eastern hemlock in the MNF witness tree database

(Thomas-Van Gundy et al., 2012). Our aim was to test use of current spodic morphology as a pedomemory proxy to portray the extent of red spruce and eastern hemlock influence in forests before mass industrial timber harvest and subsequent wildfire. Furthermore, we think that these same spatial models of podzolization can be used to connote how red spruce restoration could lead to the buildup of surface O horizons and increased forest carbon stocks and other ecosystem services.

2. Materials and methods

2.1. Study area

We examined sites in the Chemung and Hampshire geologic formations across the regional transition between temperate northern hardwood and subalpine spruce communities within the MNF (Fig. 2). These are acid geologies primarily composed of shale and siltstone parent materials with minor inclusions of sandstone (WVGES, 1968). The area is relatively moist, with mean annual precipitation ranging from 1118 to 1524 mm (44–60 in.; Arguez et al., 2012), which is likely controlled by elevation and orographic effects. Mean annual temperature ranges from 6.0 to 8.3 °C (Arguez et al., 2012), which reflect elevation, slope aspect, and cold air drainage patterns. The elevations of sites examined ranged from 880 to 1320 m, which spans the approximate elevation boundary (~1100 m) between the mesic and frigid soil temperature regimes cited as an important boundary by other regional podzol studies (Lietzke and McGuire, 1987; Stanley and Ciolkosz, 1981). The topography in the area includes flat narrow ridgetops, steep mountainsides, occasional rock outcrops, and deep and narrow river valleys. Within slopes there are benches, hollows, and spurs along with cradle-knoll micro-relief that affect how water, energy, and materials are distributed in the soil system (Schaeztl, 1990).

Current vegetation in the study area in Fig. 2 grades from northern hardwoods to spruce–hemlock forests, with mixed conifer–northern hardwood areas between. Common tree species observed in the study area include red maple, sugar maple, mountain maple (*Acer spicatum*), striped maple (*Acer pennsylvanicum*), red spruce, eastern hemlock, yellow birch (*Betula alleghaniensis*), sweet birch (*Betula lenta*), American basswood (*Tilia americana*), white ash (*Fraxinus americana*), northern red oak, black cherry, American beech, mountain magnolia (*Magnolia fraseri*), and cucumber magnolia (*Magnolia acuminata*). Commonly seen shrubs include mountain holly (*Ilex montana*), mountain laurel (*Kalmia latifolia*), and rhododendron (*Rhododendron* spp.), as well as shrubby root sprouts as a result of the beech bark disease complex (Shigo, 1972). Common herbaceous and ground cover species observed include New York fern (*Thelypteris noveboracensis*), intermediate woodfern (*Dryopteris intermedia*), hypnum moss (*Hypnum imponens*), liverwort (*Bazzania trilobata*), three *Lycopodium* species, *Viola* spp., and three *Carex* species.

2.2. Data collection and analysis

Three types of soil data were collected as part of this research: (i) extensive point observations of soil morphological properties, (ii) detailed pedon descriptions with comprehensive laboratory characterization of soil physical and chemical properties at selected sites, and (iii) fixed-area forest vegetation plots with detailed pedon descriptions and limited soil laboratory characterization data. Data collected at all visited locations included detailed field descriptions of the soil morphology at hand-excavated pits with a focus on podzol morphology. We express podzol morphology as a 'spodic intensity' (SI; Table 1) based on color, horizon characteristics, and smeariness observations typical of 'spodic soil materials' in US *Soil Taxonomy* (Schoeneberger et al., 2012; Soil Survey Staff, 1999). Data were collected by a variety of local soil scientists associated with the USDA-NRCS, USDA-Forest Service (FS), and West Virginia University (WVU). Soil descriptions were made consistent with U.S. national soil survey standards (Schoeneberger

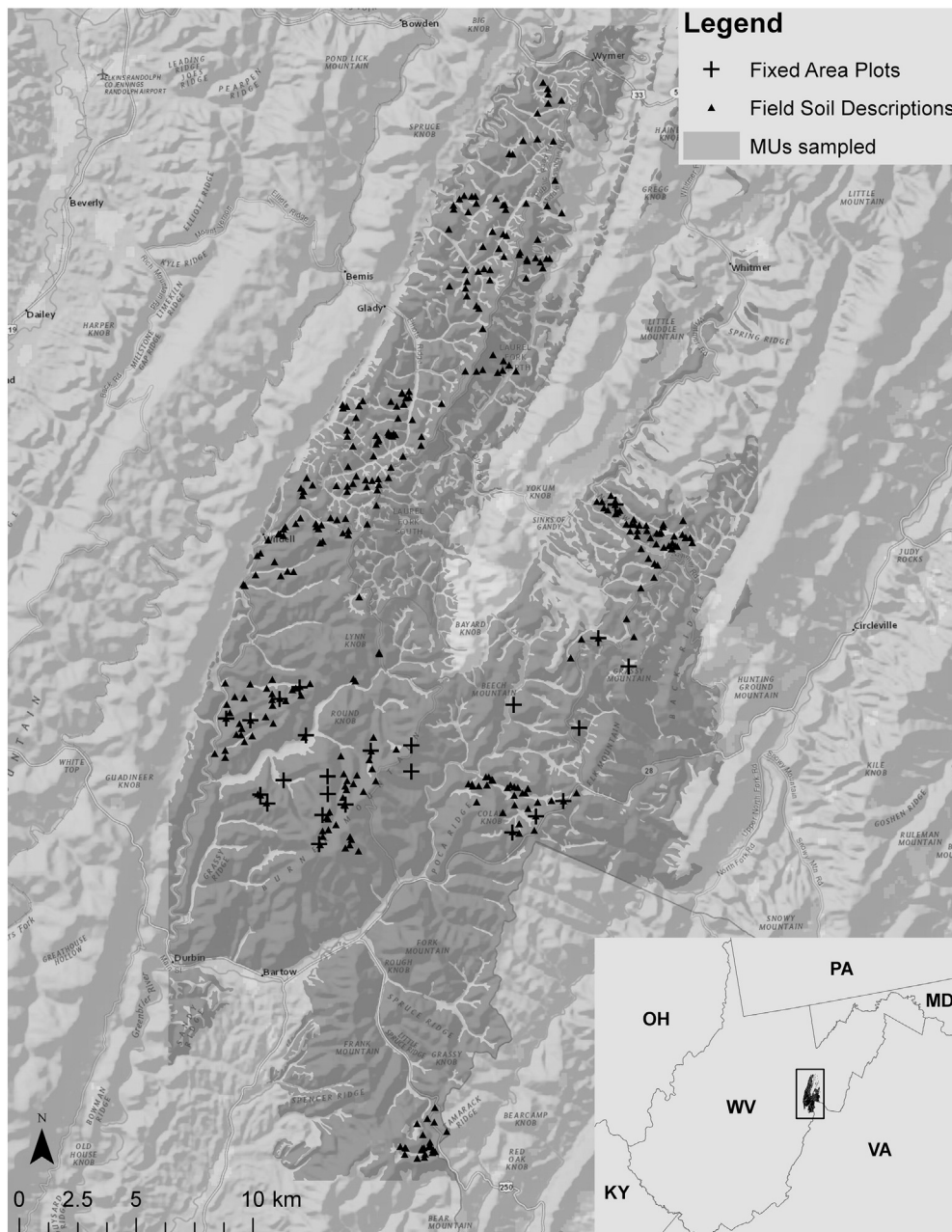


Fig. 2. Study area and data collection locations overlaid on ArcGIS 10 National Geographic mapping baselayer of local features (roads, shaded relief, cities, landmarks).

et al., 2012). Site locations were selected to evaluate soils derived from Devonian-age shale parent materials on upland landscape positions for the purpose of soil survey update and preliminary ESD reconnaissance. Specific soil map units were associated with three common soil series: Mandy (loamy-skeletal, mixed, active, frigid Spodic Dystrudepts), Berks (loamy-skeletal, mixed, active, mesic Typic Dystrudepts), and Dekalb (loamy-skeletal, siliceous, active, mesic Typic Dystrudepts). Overstory and understory vegetation species lists were also noted at every location.

The extensive point observations were obtained from 2010 to 2012 at 322 locations throughout the study area. Sampling locations were allocated in small watersheds identified by the FS for examination. Specific sample locations were identified using a stratified random sampling technique in each watershed. From within the specified Mandy, Berks, and Dekalb map units, strata were created based upon vegetation (spruce dominated or other; Lammie, 2009), slope curvature (convex, linear, or concave), and slope gradient ($>35\%$ or $<35\%$). Slope

curvature and slope gradient were calculated in ArcGIS Spatial Analyst (ESRI, 2011) using a publicly-available 3-meter resolution DEM (<http://www.wvgis.wvu.edu/data/dataset.php?ID=261>). These criteria were concatenated to produce individual strata classes (e.g., spruce-convex $\leq 35\%$ slope). Points were randomly located within each stratum using the ArcGIS random point generator. The number of points allocated to each stratum was weighted based on the relative areal amount of each stratum in the watershed. In the watersheds, the soil profiles were examined at an approximate density of one every 25 ha. A variety of handheld GPS units were used to record actual locations in the field, which makes estimating spatial error of these data difficult.

At seven locations within the study area soil pits were excavated, described, and sampled, and the samples were sent to the NRCS Kellogg Soil Survey Laboratory (KSSL) in Lincoln, NE, for full characterization of soil physical and chemical properties using standard soil laboratory procedures (Burt and Soil Survey Staff, 2004) to document the re-classification of the Mandy soil series from Typic Dystrudepts to

Table 1
Description of spodic intensity (SI) classes based on observable field morphology.

SI class	Description
0.0	No evidence of podzolization.
0.5	Very weak expression of podzolization. There is only slight physical evidence of podzolization. A slightly redder hue and higher value is present at the top of the B horizon, but the hue is less than one Munsell hue redder than an underlying horizon. The soil is non-smear ^a .
1.0	Weak expression of podzolization (spodic intergrade, very close to Spodosol). Spodic materials are present, but they might not meet the criteria for a diagnostic spodic horizon. A weakly expressed Bs horizon is present. The Bs horizon is one Munsell hue redder than an underlying horizon. Bhs material is usually absent. An albic E horizon is not present. The spodic materials are sometimes weakly smear ^a .
1.5	Moderate expression of podzolization (Spodosol). Spodic materials are present as a diagnostic spodic horizon. A moderately expressed Bs horizon is present, often with pockets of Bhs material. An albic E horizon is not present. The spodic materials are often weakly smear ^a .
2.0	Strong expression of podzolization (well-expressed Spodosol). A diagnostic spodic horizon is present usually underlying an albic E horizon. A Bhs or Bh horizon is continuous across at least 85% of the pedon. The spodic materials are often moderately smear ^a .

^a Smeariness (Schoeneberger et al., 2012, page 2–65) is a physical observation about how moistened soil samples fail when they are squeezed and rubbed between the thumb and forefinger. Smeariness can help identify spodic soil materials.

Spodic Dystrudepts, and the establishment of Wildell, a new soil series classified as Typic Haplorthods. Soil depth profiles of acid oxalate extractions of Al and Fe were compared from Mandy ($n = 4$) and Wildell ($n = 3$) as well as three similar, but non-podzolized, soils (analyzed at WVU) from the area thought to be associated with historic hardwood communities. Acid oxalate primarily extracts amorphous to poorly crystalline material including Al (e.g., Al rich allophane and imogolite type materials) and Fe (e.g., ferrihydrite) sesquioxides diagnostic of Spodosols (Burt and Soil Survey Staff, 2004). *U.S. Soil Taxonomy* (Soil Survey Staff, 1999) uses the percent weight of aluminum plus half of that of iron ($Al + 0.5Fe$) as one criterion of spodic materials, and we provide depth profiles demonstrating consistency between field spodic intensity (SI, Table 1) observations of color, spodic horizon expression, and soil smeariness (Schoeneberger et al., 2012, page 2–65) with laboratory depth profiles of $Al + 0.5Fe$.

Additionally, in 2013, 24 fixed-area forest plots centered on new soil pit observations were observed to quantitatively compare tree species composition to spodic properties and O horizon thickness. Plots were located near a subset ($n = 15$) of the 322 original locations that were easily accessible and representative of the range of variability recorded. Of the nine remaining new sites, three were located at ridgetop sites that were not represented well in the original sample, and six were randomly located in the study area. Of the 15 revisited sites only two fell within the same pixels as the 2010–2012 observations used for spatial modeling predictions, which makes even these revisited sites pseudo-independent of the original observations for validation purposes. Plot locations were all recorded with a Magellan MobileMapper Pro (v 6.52) GPS unit allowed to record in WASS mode for at least 30 min at ground level just upslope of the soil pit face at roughly the center of the plot.

Fixed, 20×20 m area plots were oriented with the slope contour. Diameter at breast height (dbh) was measured on all trees greater than 7 cm dbh. From measured dbh values and species tallies, importance values (IMP) were calculated for red spruce and eastern hemlock (Eq. (2); following Rollins et al., 2010).

$$IMP = 0.5((\text{species basal area}/\text{plot tree basal area}) + (\text{species count}/\text{plot tree count})) \quad (2)$$

Importance values are proportional measures of relative composition of a specific species that range from zero to one. To compare with IMP

values within plots, O horizon thicknesses were observed at the soil profile as well as at the center of each plot quadrant ($n = 5$ per plot). The importance of red spruce and hemlock were added to get a ‘conifer importance’ (CNIMP), which we hypothesized would show strong correlation with O horizon thickness.

We expected that conifer importance would trend positively with both spodic intensity (SI) as well as O horizon thickness. However, because reviewed studies indicate that current conifer communities are much reduced compared to pre-settlement conditions (e.g., Thomas-Van Gundy et al., 2012), we believed that CNIMP values would have a stronger relationship with O horizon thickness because the Al and Fe accumulations reflected in SI visual cues and smeariness observations are longer lived than organic carbon and O horizons in similar soils (Barrett and Schaetzl, 1998; Hix and Barnes, 1984; Lundström et al., 2000b; Parfitt, 2009). We suspected that O horizons have adjusted much more quickly to forest composition changes, and thus would maintain closer correspondence to the current forest state.

2.3. Spatial modeling using DSM

A binary random forest probability model (Breiman, 2001; Liaw and Wiener, 2002; Niculescu-Mizil and Caruana, 2005) was implemented to relate a suite of DEM and remotely sensed variables (Table 2) to soils that showed no sign of podzolization ($SI = 0$) versus those that did ($SI > 0$). All DEM variables were computed from the 1-arc second USGS National Elevation Dataset (Gesch et al., 2002; Gesch, 2007) in SAGA GIS (Conrad and Wichmann, 2011). Landsat Geocover imagery from 2000 (MDA, 2004) was also included as a potential predictor source representing current vegetation and land use. Tabulated soil observations and spatial predictor data were intersected using nearest neighbor spatial support and exported from SAGA into the R computing software (R Core Development Team, 2008) for model creation and implementation. Underlying random forest probabilities (relative ensemble votes) were exported as an xyz formatted comma delimited file and imported into SAGA GIS to map spodic morphology probability (probability of $SI > 0$).

Validation of the probability model was evaluated using three approaches. First, the randomForest R package out of bag error (oob) was reported for a model built with the full 322 field point observations. Secondly, a model of a random 2/3 subset of the field points was created and predicted onto the withheld 1/3 of the points for an independent validation. The classification accuracy and confusion matrix of the withheld data was then reported for the probability threshold that maximized overall accuracy in the validation set by trial and error. Thirdly, the 24 plots examined in 2013 were tested against the predicted surface created by the model created from the full 322 field points. Agreements between predictions and plots were reported for (i) all plots ($n = 24$), (ii) completely independent new observations ($n = 9$), and (iii) the pseudo-independent sites that were revisited, but fell into different pixels than the original 2010–2012 GPS points ($n = 13$).

The spodic probability model created from the full field observation set ($n = 322$) was then compared to the MNF witness tree database (Thomas-Van Gundy et al., 2012). Points that intersect the predictive model data footprint ($n = 1031$) were tested to see if witness sites where spruce or hemlock were reported had higher spodic probability values compared to sites with neither species recorded. Both a Welch two-sample *t*-test and a Wilcoxon rank sum test with continuity correction were used to test this hypothesis against a null of no difference in the R statistical computing program (R Core Development Team, 2008). We expected that areas predicted to have spodic morphology (higher probabilities) should correspond with areas that had more spruce and hemlock historically. We then compared our map of spodic properties with a current forest inventory (Byers et al., 2013) to determine how much of the modeled area of spodic expression is currently under hardwood dominated cover congruent with the reported historic conversion of large areas out of spruce cover.

Table 2
Spatial variables used to model spodic probability.

Variable name	Description
<i>National Elevation Dataset (~27.5-meter resolution)</i>	
NWNESS	Index from 1 to –1 of how northwest (1) or southeast (–1) a site faces
EASTNESS	Index from 1 to –1 of how east (1) or west (–1) a site faces
SOUTHNESS	Index from 1 to –1 of how south (1) or north (–1) a site faces
NENESS	Index from 1 to –1 of how northeast (1) or southwest (–1) a site faces
ELEVm	Elevation in meters
PLAN_CURV	Curvature perpendicular to the slope direction
PROF_CURV	Curvature parallel to the slope direction
LS_FACTOR	Slope-length factor from USLE as calculated in SAGA GIS
CONVERGENCE	Overall measure of concavity
SLOPEPOS	Index from 0 (valley floor) to 100 (ridgetop) of slope position (Hatfield, 1996)
SLOPE	Slope gradient (rise/run) in fraction units
MRRTF	Multiple resolution ridgetop flatness index
MRVBF	Multiple resolution valley bottom flatness index
TWI	Topographic wetness index
ALT_OVER_STREAM	Altitude above local stream channel
BASELEVEL	Elevation of nearest channel point to each pixel in its given watershed
CONTRIBAREA	Upstream contributing area
REL_HT_1	Height of cell above the local minimum elevation in 1-pixel radius
REL_HT_2	Height of cell above the local minimum elevation in 2-pixel radius
REL_HT_3	Height of cell above the local minimum elevation in 3-pixel radius
REL_HT_5	Height of cell above the local minimum elevation in 5-pixel radius
REL_HT_10	Height of cell above the local minimum elevation in 10-pixel radius
REL_HT_20	Height of cell above the local minimum elevation in 20-pixel radius
REL_HT_30	Height of cell above the local minimum elevation in 30-pixel radius
REL_HT_50	Height of cell above the local minimum elevation in 50-pixel radius
REL_HT_70	Height of cell above the local minimum elevation in 70-pixel radius
<i>Landsat Geocover 2000 (14.5-meter resolution, resampled to 27.5-m)</i>	
NIR	Near Infrared band in 8-bit digital number units
MIR	Middle Infrared band in 8-bit digital number units
GREEN	Green visible band in 8-bit digital number units
MIRNIR	Ratio of MIR/NIR
GREENNIR	Ratio of GREEN/NIR
GREENMIR	Ratio of GREEN/MIR

3. Results

3.1. Soil profile data

Acid oxalate extractable Al and Fe in soil depth profiles clearly distinguished field SI observations representing the gradient of spodic soil morphologies seen in the study area (Fig. 3). Analyzed profiles exhibited distinct depth profiles of Al + 0.5Fe acid oxalate extract, which is one of the criteria for Spodosol classification in U.S. *Soil Taxonomy*. Some variation in depth ranges and intensity of peaks within the classes existed, but overall graphed patterns appeared to separate soils by SI class well. The lack of an increase in Al + 0.5Fe in the subsoil of the non-spodic data contrasts strikingly to other sites, which provides evidence supporting our decision to separate these sites from the others in our spatial models of spodic expression presence.

3.2. Spatial models of spodic probability

Spodic probability spatial models (Fig. 4) had overall error rates of 30% for both out-of-bag error and the one-third withholding validation. The validation results using withheld data indicated a maximum classification agreement at a 0.57 probability threshold to separate spodic from non-spodic predictions and indicated that predictions of spodic sites were more reliable than those of non-spodic sites (Table 3). The weaker prediction agreement of non-spodic sites (46.3% user error, 61.3% producer error, Table 3) with a lower user error rate indicates that non-spodic sites were over predicted relative to spodic sites. At fixed area forest plots the error rate was 12.5% for all plots ($n = 24$), 22.2% for strictly independent plots ($n = 9$), and 7.7% for the pseudo-independent site revisits that fell into separate pixel predictions than original soil descriptions. Based on these different metrics, 70% seems to be a consistent conservative estimate of overall prediction accuracy.

3.3. Environmental controls on spodic probabilities

Slope aspect, mid-infrared (MIR) band of Landsat Geocover, and topographic flow convergence calculated in SAGA GIS were the four most important variables in the randomForest analysis of mean decrease in accuracy when these variables were omitted from model building. Specifically, the EASTNESS and NWNESS slope aspect variables were the most important followed by MIR, and CONVERGENCE. Visual evaluation of the map output (Fig. 4) indicated that W–NW aspects had higher spodic probability, but other factors were more subtle. A highly pruned classification tree was built in rpart (Therneau et al., 2010) to further help interpretations (Fig. 5). Tree structure shows very similar results to the random forest model, with western aspects most favoring spodic development followed by lower MIR values where imagery picks up conifer canopy (usually in lower slope positions of deep narrow valleys that cut into the mountains). The LS_Factor is a water flow energy term from the Universal Soil Loss Equation that SAGA will calculate from a DEM. It is very similar to the CONVERGENCE variable and both mainly distinguish areas that likely concentrate overland water runoff energy. The LS_Factor split might be indicative of past erosion eliminating some areas of spodic expression that might not represent historic spruce preferences, and only isolates 4.2% of the spodic sites. The confusion matrix of the classification fit shows that these three environmental variable splits correctly classify 75% of the soil descriptions.

3.4. Witness tree comparison

Comparisons of spodic probabilities at witness tree points showed a positive shift in the distribution of values at sites where hemlock or spruce were listed (Wilcoxon rank sum, $p = 0.0052$; Welch 2-sample t -test, $p = 0.0077$; Fig. 6). This shift was highly significant statistically,

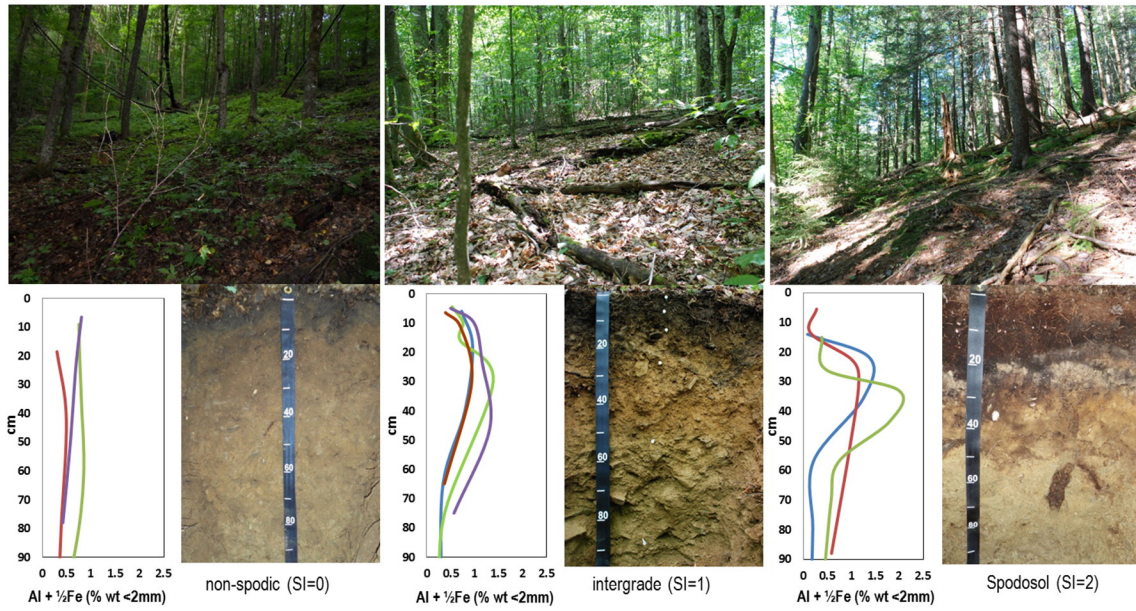


Fig. 3. Examples of site conditions, soil profiles, and acid oxalate data of the non-spodic hardwood ecological site (SI = 0), spodic intergrademixed forest (SI = 1), and spodic conifer forest (SI = 2). Green line within graphs represents pictured soil profile. Pictures are of current vegetation at the pictured profile. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

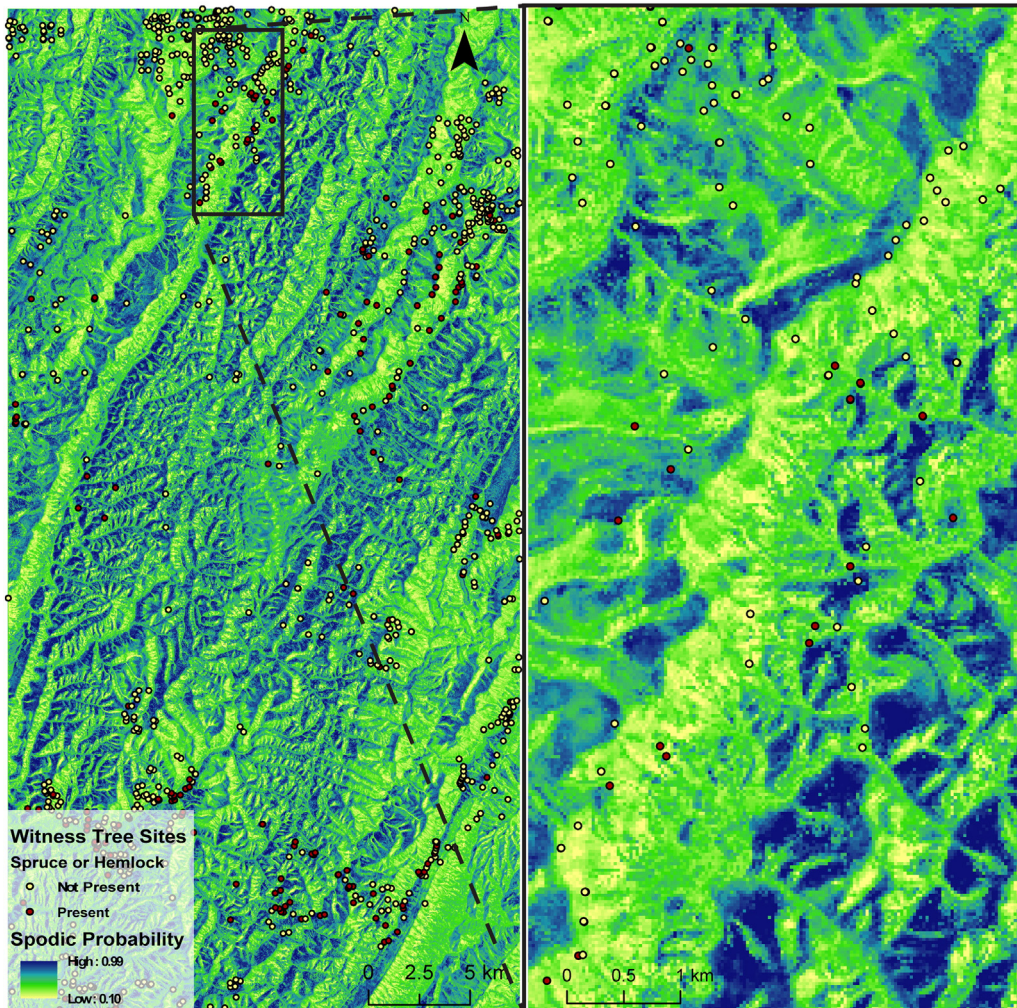


Fig. 4. Spodic morphology probability map with witness tree points overlaid.

Table 3
Confusion matrix from withheld 1/3 validation set for spodic probability predictions using a 0.57 threshold for classification as 'spodic'.

		Predicted		
		Non spodic	Spodic	
Observed	Non spodic	19	12	61.3%
	Spodic	22	61	73.5%
		46.3%	83.6%	70.2%

and while the magnitude of the shift is visible in the distribution, it still exhibits considerable distribution overlap. However, this area represents a transitional gradient between hardwood and conifer that we think produces a concurrent gradient of spodic expression and thus considerable overlap in distribution would be expected logically. Witness tree records are also not exhaustive species listings, and an omission of a species does not indicate that it was not present. We must also account for the imperfect spodic spatial model, which does not account for ~30% of the soil variability.

3.5. Conifer importance and soil morphology

Conifer importance at forest plots shows positive associations with both the thickness of O horizons and SI values. However, the trends with O horizon thickness are much more consistent indicating support for our hypothesis of a quick O-horizon response to forest change (Fig. 7). Both graphs of O horizon response have a positive trend with conifer importance, with overall responses of 0.96 to 1.1 cm of O horizon thickness increase per 10% of conifer importance increase. It is

important to note that conifer importance does not include any calculation of site productivity, it is solely based on the relative composition of tree species. Therefore, this association is somewhat independent of site productivity. Interestingly, for our conifer dominated plots older than 100 years in averaged tree core ring counts (n = 3 per plot), O horizon thickness averages 18.8 cm compared to the overall regression average of 15.8 cm, suggesting that over time O horizons may get even thicker similar to the findings of Schaetzl (1994). At those older plots, we observed only one site with no charcoal evidence of past fire, and the average O horizon thickness was 26.8 cm with a maximum of 37 cm. This might be suggestive of the true old growth condition; however, relatively undisturbed sites are hard to find due to the prolific extent of historic disturbance and thus it is difficult to establish a representative sample.

4. Discussion

Our results demonstrate the importance of understanding the ecological soil factorial (Eq. (1); Amundson and Jenny, 1991, 1997; Jenny, 1961, 1980) and its relationship to pedomemory. Soil process pathways driven by vegetative influences that manifest themselves in soil morphology can inform our understanding of the ecological history and plausible management responses of a site (Higgs et al., 2014; Johnson and Watson-Stegner, 1987; Phillips and Marion, 2004; Schaetzl and Anderson, 2005; Schaetzl and Schwenner, 2006; Lin, 2011; Simonson, 1959; Targulian and Goryachkin, 2004). We demonstrate this in the Central Appalachian northern hardwood-red spruce transition using models of spodic morphology tested against historic land deed witness tree data.

We think that our findings are also important globally because they bring together independent evidence supporting use of soil properties to map historic reference communities. The concept of carefully selecting pedomemory or pedogenic attributes to help understand

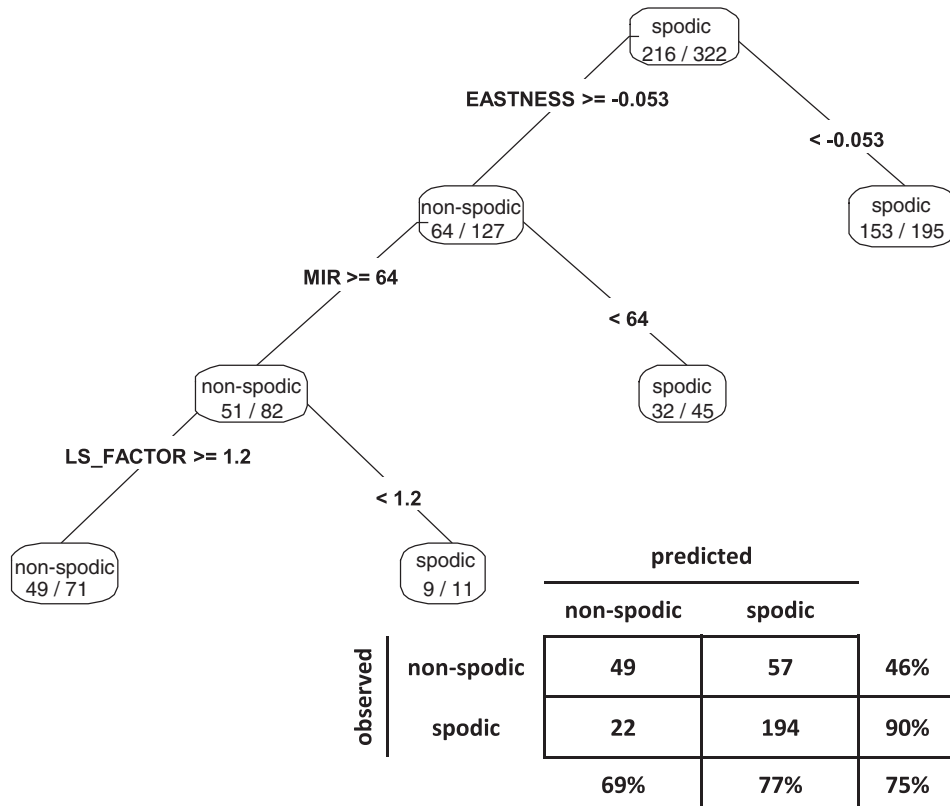


Fig. 5. Classification tree showing how GIS variable splits can isolate more and less spodic groups of soil observations. Correct predictions over total node set size are shown under classification labels (e.g., spodic, 153/195 on upper right leaf). The confusion matrix of the fitted data is shown under the tree.

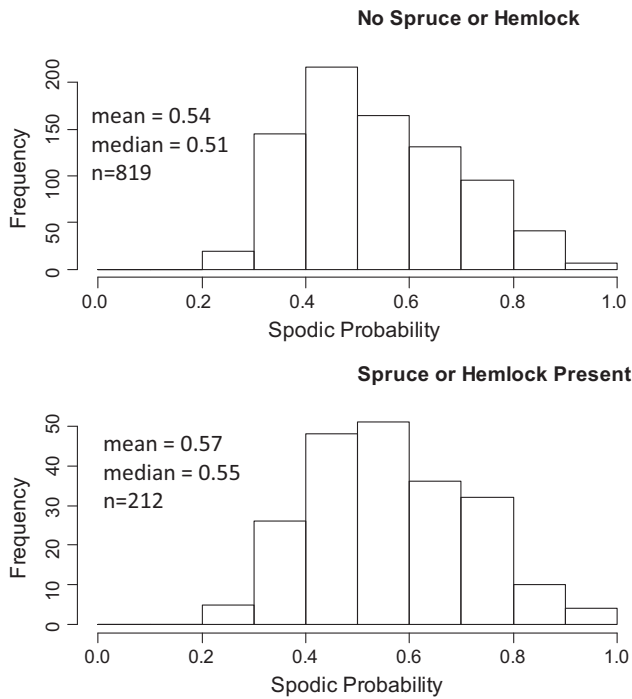


Fig. 6. Spodic model probabilities at witness tree sites where no spruce or hemlock were recorded (top), and where spruce or hemlock were observed (bottom).

vegetation dynamics over time is not limited to these systems. For example, recent studies in Australia have shown geochemical pedogenic linkages to vegetative and hydrological dynamics and diversity that generally relate to pH, mineralogy, and redoximorphic features (Bui et al., 2014; Coventry et al., 1983; Coventry and Williams, 1984; Fritsch and Fitzpatrick, 1994; Laliberté et al., 2014; Múcher and Coventry, 1993). There are many ecosystems that promote certain soil morphologies that have been converted to other land uses with different influences on soil (Goldewijk, 2001; Hansen et al., 2013; Johnson and Watson-Stegner, 1987; Karhu et al., 2011; Miles, 1985). These land use changes include deforestation, forest type conversions, agricultural expansion, and urbanization. Changes are often complex and hard to recreate when detailed historic records don't exist, which makes soils invaluable recordings of site histories (Targulian and Goryachkin, 2004).

Our results suggest that the disturbance in the mountains of WV resulting from extensive past industrial timber harvest and related fire, and resulting forest composition changes, probably caused large losses of soil carbon stocks in the forest floor. However, the fact that O-horizons seem to have already somewhat adjusted to current forest composition seems to indicate that red spruce restoration has the potential for re-accumulation of large amounts of forest floor (and thus organic carbon). Earlier work on the spruce-hardwood ecotone in Vermont also showed a correspondence between more acidic soils with deeper forest floors and red spruce dominated areas, but didn't report as much specificity between spruce and spodic properties (Siccama, 1974; Young, 1934). However, modern studies must account for the possibility that the vast harvest disturbance of forests associated with European colonization has favored hardwood incursion into formerly conifer influenced areas (Nowacki et al., 2010; Pielke, 1981) that might be reflected in spodic soils currently under hardwood cover.

When our spodic probability map was overlaid on a current forest inventory map recently completed by Byers et al. (2013), much of the modeled spodic areas were under hardwood cover (<10% conifer). Of areas of the spodic model with >70% probability (26% of study area),

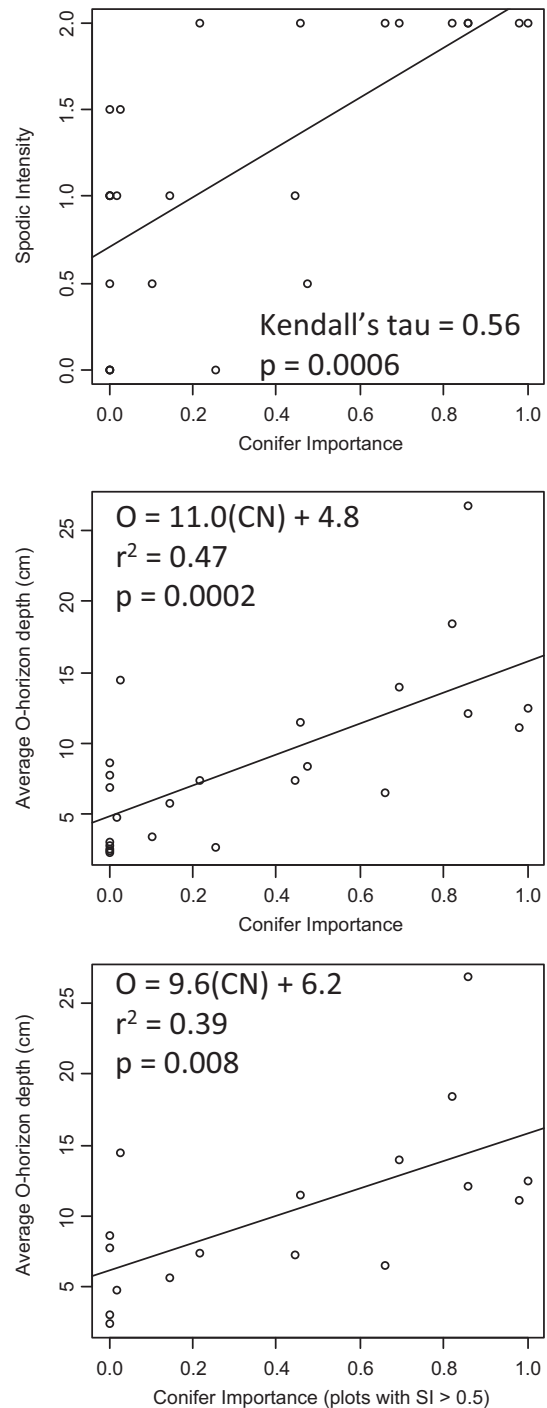


Fig. 7. Relationships between conifer importance (CN) with spodic intensity (top) and O horizon thickness in all plots (middle) and at plots with SI of 1–2 (bottom). Kendall's Tau is used to evaluate the SI graph because it is an ordinal data type.

68% were mapped by Byers et al. (2013) as hardwood. This represents a large area of forest currently dominated by hardwoods that we postulate were dominant or co-dominant spruce or hemlock cover before railroad era disturbance. The 70% threshold was chosen because at that probability level we had even greater confidence in our prediction of spodic property presence (77% using withheld validation set), and the vast majority of fully expressed Spodosols (SI = 2) observed at forest plots (100% of plots with Spodosols) and field validation sites (71% of field transect sites with Spodosols) were also seen at probabilities >70%.

4.1. Understanding historic red-spruce community distribution and spodic soil properties

Other studies of the red spruce — northern hardwood ecotone have often focused on the elevation of the transition and the associated ecological changes (Siccama, 1974; Beckage et al., 2008). Late twentieth century decreases in the growth of red spruce and upward shifts of the ecotone have largely been attributed to climate warming, but cannot rule out pollution and competition as co-factors (Beckage et al., 2008; McLaughlin et al., 1987). Hamburg and Cogbill (1988) were able to show that climate was probably more influential than air pollution (e.g., acid rain) in red spruce decline since 1800. However, all of these changes in red spruce population are superimposed upon the historic harvest impacts, and make determining pre-industrial population distribution estimates quite complex. This complex history makes a plausible pedomemory proxy attractive.

Although we were able to demonstrate strong statistical evidence of spatial correspondence between modeled spodic soil properties and historic witness tree red spruce and hemlock occurrences, the underlying spatial model covariates also seemed to indicate similar climate-related topographic controls to those of red spruce witness trees. We compared analysis from Thomas-Van Gundy et al. (2012) with our models and found similar topographic relationships. Our field data were taken from the Northern High Allegheny Mountain (NHAM) area, but the spodic model footprint we tested also included areas and witness tree locations from smaller areas of the Southern High Allegheny Mountain (SHAM) and Western Allegheny Mountain (WAM) areas as analyzed by Thomas-Van Gundy et al. (2012). In their analysis of spruce locations in NHAM, SHAM, and WAM, Thomas-Van Gundy and co-authors showed spruce associations with northern slope aspects, with northwest slope aspects being specifically being favored more in NHAM and SHAM. They also found that relative elevation and landform preferences were for higher ridgetops in SHAM, more cove-like settings in NHAM, and lower valley bottoms in WAM. Our models showed that spodic soils were most probable on west–northwest slope aspects, similar to the witness tree database. Spodic morphology was also associated with low MIR pixel values that corresponded with conifer-dominated plots (Wilcoxon rank sum test, $W = 89$, $p = 0.0324$, alternative of MIR being lower at sites with conifer importance $>50\%$). These same low MIR values were also associated with lower slope positions that typically depict coves and narrow valleys (SLOPEPOS in Table 2; Wilcoxon rank sum test, $W = 108$, $p = 0.013$, alternative of lower MIR at lower slope positions). These areas with low MIR values seem to be representing remnant spruce populations in coves and at lower elevation narrow valley bottoms analogous to the landform analysis seen at lower elevations by Thomas-Van Gundy et al. (2012). We summarize our postulated topographic–climate relationships in Fig. 8. It includes an elevation gradient that starts with dominant spruce on the high ridgelines, and grades into spruce microclimates on cool–wet aspects at mid-elevations, and strongly sheltered cold air drainages at lower elevations.

It is important to recognize that our observations only cover a part of the NHAM area analyzed by Thomas-Van Gundy et al. (2012). Our points cover the more rugged ridges and narrow valleys of the upper Greenbrier River watershed and Middle Mountain that run in a mostly S–SW to N–NE direction. Other parts of NHAM, like Canaan Valley, which sits on top of the Blackwater Falls anticline and weathered limestone, have a variety of ridge orientations and more open topography. We also included eastern hemlock as a red spruce associate in witness-tree comparison, which could also be slightly shifting our model results relative to Thomas-Van Gundy et al. (2012), whose analysis was specific to red spruce.

Overall, we feel that these topographic controls probably indicate cooler and wetter climatic niches. Middle elevations (~1000–1250 m) in the WV historic red spruce range seem to have narrower climate windows that exclude spruce–hemlock conifer dominated stands from

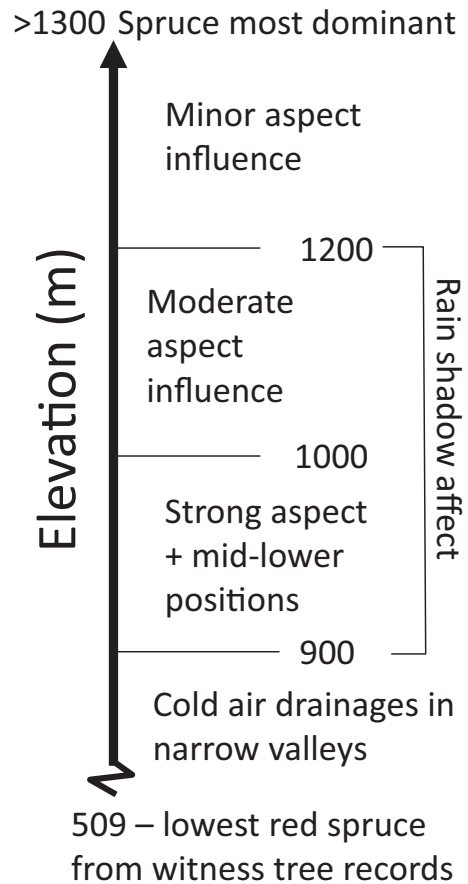


Fig. 8. Conceptual diagram of how climatic and topographic controls of red spruce appear to change over elevation.

southeast–east aspects that are warmer and drier, which is likely a result of orographic rain-shadows and greater solar insolation. We also think that the presence of spruce preferentially in narrow valley bottoms and toeslopes at lower elevations is probably related to cold air drainages where we also observed more persistent fog that probably favors spruce. Recent maximum entropy (MaxEnt) models of red spruce habitat suitability indicate that cooler temperatures (especially summer temperatures) and higher snowfall and precipitation were most important in predicting potential red spruce habitat, but did not identify slope aspect as a major driver (Nowacki and Wendt, 2010; Beane et al., 2013). It is difficult to determine if slope aspect-related climate variability was detected in the climate layers used by these studies because the base data for those spatial layers had 400-meter and 1-km resolution, and was probably too coarse to pick out many fine scale topographic aspect patterns. These MaxEnt models also did not detect the lower valley bottom populations of red spruce found down to below 600 m in the witness tree database. However, our model did extrapolate spodic predictions into those lower areas, and a significant portion of the witness-tree points we tested against were located below 800 m in areas near Bowden, WV (upper left corner of Fig. 4), which seems to indicate that our spodic model detected these areas of historic spruce found at lower elevations.

Interestingly, soil variables were included in the MaxEnt models as well as the witness-tree studies. In all studies, USDA-NRCS soil surveys, including the more generalized State Soil Geographic (STATSGO2) database and the more detailed Soil Survey Geographic (SSURGO) database soil maps, were summarized by map unit, which can produce interpretation issues where multiple soils are grouped into one map unit (Nauman and Thompson, 2014; Nauman et al., 2012; Thompson et al., 2012). However, the Mandy soil series was identified as associated

with spruce witness tree locations, and was recently reclassified to include recognition of spodic properties based on data used in this study. Many of the other soils identified by Thomas-Van Gundy et al. (2012) are also likely to be cool-moist variants of Inceptisols and Ultisols that might need to be re-evaluated for re-classification as spodic subgroups or Spodosols. For example, the Shouns soil series was found to be associated with spruce in parts of MNF. We found a Shouns soil profile sampled on the southern side of Spruce Knob and characterized by the NSSC that had a discernable depth peak in acid-oxalate extracted Al and Fe (Pedon ID S03WV-071-001, NCSS, 2014). Notably, the two Spodosols previously mapped in WV (Leetonia and Gauley), which are almost exclusively associated with current red spruce stands (Delp, 1998; Flegel, 1998; Losche and Beverage, 1967; Williams and Fridley, 1931; USDA-SCS and USDA-FS, 1982), were not mentioned in the witness tree paper. Beane et al. (2013) did note associations with STATSGO2 soil map units that included Gauley as well as other similar soils to the witness tree results. Nowacki and Wendt (2010) noted associations with shallower soils and fragipans, which makes intuitive sense because red spruce is shallow rooted and perhaps better adapted to fragipans than other species. Nowacki and Wendt (2010) also discussed the likelihood of spodic soil properties being associated with red spruce, which partially inspired this study, but the SSURGO data available for their analysis at that time did not reflect that relationship.

4.2. Future implications

More laboratory corroboration and wider spatial sampling would provide greater certainty for our conclusions regarding historic forests and restoration projections in WV. We did not include data describing soil organic carbon dynamics in mineral soil horizons (A, Bh, and Bhs) at these sites to see how restoration might affect those pools, but we think that they could also represent a significant potential flux after disturbance. Others have shown that mineral horizon organic carbon stocks can be lost via depodzolization after disturbance and vegetation conversion in similar systems (Barrett and Schaetzl, 1998; Hole, 1975). Soil pools, along with calculations from forest growth model scenarios (e.g., Krankina et al., 2012; Schulze et al., 2012) could provide a more interdisciplinary illustration of carbon sequestration potential and will likely provide evidence of even greater ability of these forests and soils to mitigate climate change.

We also hope that other researchers will further investigate subalpine/boreal conifer to temperate hardwood ecotones throughout other comparable zones of the world to see if similar scenarios exist where prior disturbance has caused compositional and biogeochemical shifts. We also expect that that future work with quantitative analysis of translocated soil sesquioxides in WV and similar areas, especially Al-rich allophanes and proto-imogolites, could potentially provide a spatially explicit map of quantitative estimates of pre-disturbance forest composition since these compounds have longer residence times in the soil than other spodic properties (Lundström et al., 2000b; Parfitt, 2009).

5. Conclusions

Soil properties and morphology can reveal pedomemory insights into past vegetative dynamics. The key to this is understanding the time scale and mechanisms associated with different vegetation related soil processes that manifest in soil development. In cool, moist, and acidic conifer forests, persistent subsurface sesquioxide horizons reside in soils for long periods and can serve as indicators of those forest communities. Contrastingly, organic carbon pools can shift quickly when forest composition is changed due to disturbance. Carbon pools that respond quickly to forest restoration represent an important potential avenue of carbon sequestration and habitat renewal. Although there is uncertainty regarding future effects of climate change on red spruce, there might be a significant mitigation potential in red spruce

restoration. Alternatively, if red spruce is lost, similar species that promote podsolization including other selected *Tsuga*, *Larix*, *Picea*, *Pinus*, and *Abies* species could serve as alternatives. Restoration of red spruce and similar carbon-sequestering species represents one of many potential climate and ecological degradation mitigation options that society will need to evaluate in our efforts to balance our global carbon pools and disturbance footprint.

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