Plant Ecol (2017) 218:305–316
DOI 10.1007/s11258-016-0687-5

Regional- and watershed-scale analysis of red spruce habitat in the southeastern United States: implications for future restoration efforts

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Received: 25 February 2016 / Accepted: 8 December 2016 / Published online: 22 December 2016

Abstract Red spruce (*Picea rubens*) is an evergreen tree with a range from Canada to North Carolina that provides habitat for multiple rare, endemic species. Red spruce-dominated forests once covered over 600,000 ha in the southeastern US, yet currently occupy a small fraction of their historical range due largely to logging that began in the nineteenth century. To combat this loss, restoration groups have emerged to actively improve the health and areal extent of red spruce. This study was conducted to (1) predict how suitable habitat for red spruce in the southeastern US is expected to change by the year 2100 in response to increasing global temperatures and (2) illustrate how these predictions can be used, in concert with local-scale information, to support efforts to restore red spruce in this region. Red spruce currently occupies a small fraction of the area indicated by our model to be suitable. The area of habitat supportive of red spruce was projected to decline from present day to the year 2100, but the magnitude of this decline depended on the level of carbon emissions, and there was considerable variability between climate models. In our case-study watershed, suitability for red spruce is predicted to decline by 2100, but may still support red spruce under optimistic to moderate emissions scenarios. At this scale, restoration strategies should also take into account locally varying conditions such as the current distribution of red spruce and competitive shrubs that may inhibit growth.

Keywords *Picea rubens* · Climate change · Pedomemory · Restoration

Communicated by James D. A. Millington.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-016-0687-5) contains supplementary material, which is available to authorized users.

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Introduction

Forests dominated by red spruce (*Picea rubens*) historically covered ca. 600,000 ha of West Virginia, but now occupy fewer than 10,000 ha of the historical range (Hiltz 2012; Lewis 1998; Rentch et al. 2007, 2010; Griffith and Widmann 2003). The decline in areal extent of red spruce in West Virginia is due largely to logging in the late nineteenth and early twentieth centuries (Hamburg and Cogbill 1988; Lewis 1998; Hiltz 2012; Rentch et al. 2007), and is emblematic of red spruce losses across the southeastern US. Red spruce provide habitat for the endangered Cheat Mountain salamander, the recently delisted Virginia northern flying squirrel and numerous rare flora and fauna (Rentch et al. 2007; Byers et al. 2010). Consequently, the maintenance and recovery of red spruce is a significant conservation concern, both for the intrinsic value of this once-plentiful species and the value of the ecosystem it supports (Stehn et al. 2011).

Conservation groups, such as the Central Appalachian Spruce Restoration Initiative, promote restoration initiatives including allocation of lands to state and federal protection, planting red spruce seedlings, and managing stands to favor regrowth of red spruce (Buckley 2014). However, for restoration efforts to be impactful, they must be based on sound science that considers both an accurate estimate of the extent and functioning of a former reference state, an ecological grounding for the definition of that reference state (Young et al. 2001; Nauman et al. 2015), and how the current system will be impacted by future climate change (Harris et al. 2006; IPCC 2013).

Recently, red spruce has begun to recover and slowly increase in areal extent (Madron 2013), but climate change may prevent continued recover (Iverson et al. 2008; Potter et al. 2010). Already near the margins of its climatic tolerance, increases in temperature and decreases in precipitation and cloud immersion increase tree stress and threaten to make portions of the current red spruce range inhospitable (Iverson et al. 2008; Potter et al. 2010; Beane and Rentch 2015).

Today, red spruce in the Central Appalachians are largely confined to cold, wet environments at high elevations, in part reflecting areas that could not easily be logged (Houle et al. 2012; Rentch et al. 2010; Thomas-Van Gundy et al. 2012; Kosiba et al. 2013). Red spruce is ecologically constrained by climate, soil characteristics, topography, and community interactions (White and Cogbill 1992; Koo et al. 2014). In the Southern and Central Appalachians, red spruce is close to the edge of its climatic suitability (Houle et al. 2012). Physiological studies indicate that the maximum photosynthetic rate is attained at air temperatures 15–20 °C, and that the photosynthetic rate is substantially reduced above 25 °C (Alexander et al. 1995). Air temperatures exceeding 32 °C cause large drops in photosynthesis and stomatal conductance (Day 2000), and can cause irreversible foliar injury (Fincher and Alscher 1992; Vann et al. 1994). Similarly, soil surface temperatures above 33 °C may damage seeds (Baldwin 1934).

Red spruce favors generally shallow, infertile soils, as these soils allow for more successful seedling survival and deter more competitive hardwood species. Red spruce seedlings have shallow, finely branched rootlets that derive all of their nutrients and water from the surface organic layer. There is a strong association between red spruce and soil podsolization (Nauman et al. 2015), with red spruce occurring mainly on acidic spodosols, inceptisols, and to a lesser extent certain histosols. Shallow organic soils with soil pH ranging from 4 to 5.5 on rocky slopes or wet, bottomland areas—places generally unfavorable to many other species—offer optimal habitat for red spruce. Red spruce occurs at elevations between 900 and 1980 m, and in Southern Appalachia Fraser fir often replaces red spruce at higher elevations (Sullivan 1993).

Where climate, topography, and soil characteristics favor red spruce, its distribution is affected by seed dispersal and seedling establishment. Seeds are produced after the tree has reached 30–40 years old, and the possible rarity of seed dispersal further than 100 m from the parent tree (Randall 1974; Dumais and Prevost 2007) suggests the current distribution of red spruce is a limiting factor in regeneration (Hughes and Bechtel 1997; Cavallin and Vasseur 2009). Rates of seedling establishment are influenced by resource competition, particularly with fast-growing shrub species such as *Rhododendron* (Byers et al. 2010). These shrubs proliferate in canopy openings, preventing the establishment and release of spruce (Horton et al. 2009; Nilsen et al. 1999, 2001; Stehn et al. 2011; Dumais and Prevost 2007). Rhododendron inhibit tree seedling establishment and growth through direct and indirect competition for nutrients, light, and water, and by changing soil chemistry and nutrient availability (Phillips and Murdy 1985; Clinton and Vose 1996; Van Lear et al. 2002; Atkins et al. 2015). Natural and anthropogenic disturbances have led to the expansion of rosebay rhododendron (*Rhododendron maximum*) thickets throughout the Central and Southern Appalachians (Phillips and Murdy 1985; van Lear et al. 2002).

Continued climatic warming has been identified as an existential threat to red spruce in the Central Appalachians (Iverson et al. 2008; Potter et al. 2010; Beane and Rentch 2015). A number of studies apply the related approaches of species distribution modeling, climatic envelope modeling, or environmental niche modeling to project the potential distribution of red spruce in space and time (Iverson et al. 2008; Potter et al. 2010; Madron 2013). Taken together, these studies predict that climate change will cause the range of red spruce in this region to retract over the next century, and potentially lead to regional extinction. Despite these dire predictions, recent increases in red spruce cover in West Virginia (Madron 2013) suggest the potential for recovery of at least a portion of the historical red spruce extent. In light of climate change, it is an open question whether such gains can be maintained over the long term, but the likelihood of success may be improved by well-planned restoration efforts that invest in sites having conditions that are well-suited to red spruce under both current and future conditions.

Regional maps documenting current red spruce coverage, for example over the Allegheny Mountains of West Virginia (West Virginia Division of Natural Resources, WVDNR 2013) can assist restoration efforts; however, the fairly coarse resolution of these maps may not reflect local, finer-scale variations in red spruce density and distributions. This may be detrimental to the planning of restoration projects, which tend to be limited in their geographic scope and must necessarily contend with local-scale variations in site quality. Additionally, few studies have analyzed how environmental conditions influencing the health and distribution of red spruce vary at this scale. High-resolution, watershed-scale maps of red spruce coverage and suitability, linked to projections of future climate, could be used to develop watershed-specific restoration plans that improve planting efficiency and the likelihood of restoration success.

In this study, we develop red spruce suitability maps under current and projected future climatic conditions at two spatial scales: (1) a region-wide analysis of red spruce habitat in the southeastern US, and (2) a small (374 ha) first-order watershed near Canaan Valley, West Virginia. A primary goal of the local-scale analysis is to demonstrate how our regional-scale analyses could be integrated with local ecological characteristics to inform restoration activities. Suitability mapping and modeling have become useful tools in guiding restoration efforts (Koo et al. 2014, 2015), and we seek to add to these works through the inclusion of newly published, highly spatially resolved, downscaled climate projections into our model of future suitability. Our work differs from other analyses of the future potential range of red spruce in that it relies on projections of its historical range rather than its current distribution (Iverson et al. 2008; Beane and Rentch 2015).

Methods

To predict the current and future potential for restoration of red spruce, we took the approach of quantifying constraints on red spruce establishment and growth, and using maps and spatially explicit climate projections to derive a suitability index for red spruce in space and time. Because spatially detailed records of the total historical extent of red spruce are unavailable, we use an empirical model to estimate the historical extent of red spruce based on the occurrence of the spruce-associated spodic soils. We then evaluate how this extent is constrained under current climatic conditions and under projected climatic conditions for the year 2100. Our climate projections reflect three emissions scenarios [representative concentration pathways (RCPs); Meinshausen et al. 2011].

We address changing suitability for red spruce at the regional scale, and then demonstrate the integration of fine-scale factors affecting the health and restoration of red spruce with a case study of a small watershed. The Weimer Run Watershed is a 374 ha watershed located within the Little Canaan Wildlife Management Area in the Allegheny Mountain range in northeastern West Virginia (39.1175, −79.4430). The watershed has an elevation range of 940–1175 m, mean annual precipitation of 1450 mm $year^{-1}$, mean daily maximum July temperature is 18.8 °C, and the mean daily maximum January temperature is −3.9 °C (Atkins et al. 2015). The watershed is a mixed northern hardwood coniferous forest with yellow birch and red maple as the dominant overstory species, with a prominent shrub understory of rosebay rhododendron (Fortney 1975; Atkins *unpublished data*). Red spruce occurs sparsely and primarily at high elevations. The watershed is located in an area with active red spruce restoration programs. At this local spatial scale, we consider how climate change and the current distribution of red spruce and competing *Rhododendron* shrubs influence restoration efforts.

Mapping regional-scale suitability

Our study is focused on the Blue Ridge, Ridge and Valley, and Central Appalachians ecoregions of

Virginia, West Virginia, North Carolina, and Tennessee. Extant red spruce are present in these ecoregions. We first estimated the historical extent of red spruce in our study area by applying an empirical model that uses topographic characteristics and satellite imagery to predict the occurrence of spodic soils closely associated with red spruce forests (Nauman et al. 2015). The model takes a decision-tree approach to assign probabilities of historical red spruce occurrence to locations based on aspect (eastness), slope factor, and solar reflectance in the mid-infrared range. Eastness is a cosine linearization of aspect, and was derived from a digital elevation model (DEM; United States Geological Survey 2009) using ArcGIS (ESRI, Redlands, CA). The slope-length factor, a water flow energy term from the universal soil loss equation distinguishing areas that likely concentrate overland runoff (Nauman et al. 2015), was derived from the same DEM using SAGA GIS (Conrad et al. 2015). Reflectance in the mid-infrared wavelengths (2.09–2.35 nm) was obtained from a 1990 Landsat GeoCover Mosaic (MDA 2004). Although the original model (Nauman et al. 2015) used the 2000 Landsat GeoCover Mosaic, part of our study area was obscured by cloud cover in the 2000 product and so we opted for the 1990 version. Based on reports of the historical extent of red spruce, we restricted application of the model to areas >900 m in elevation. Source datasets were assigned a common projection (UTM Zone 17N, datum WGS 1984) and resampled from their native resolution to 885 × 885 m grid cells, matching the resolution of the climate projection datasets.

Climatic constraints on red spruce were evaluated based on mean (historical or projected) July daily maximum temperatures. We focused on this variable because it provides an index to the amount of thermal stress potentially faced by red spruce in a given location, and because it has previously been shown to be predictive of the distribution of red spruce (Iverson et al. 2008). Cold winter temperatures may damage red spruce (Dumais and Prevost 2007); however, given where it occurs on the landscape this is unlikely to place strong constraints on the distribution of red spruce in the southern portion of its range, and given the warming trend of climate, any negative effects of cold temperatures on red spruce in this region are likely to diminish.

We assessed current and future climatic constraints on red spruce by creating a climatic suitability scale ranging from 0 to 1 based on its physiological response to high temperatures (Alexander et al. 1995; Baldwin 1934; Day 2000; Vann et al. 1994). Locations with July daily maximum temperatures <25 °C were assigned a value of 1, and those >32 °C were assigned a value of 0. In locations where the July daily maximum temperature was between 25 and 32 °C, we assumed a linear decline in the performance of red spruce, resulting in suitability index values following the function $s_{i,j} = 1 - (t_{i,j} - 25)/(32 - 25)$, where $s_{i,j}$ is the suitability index, and $t_{i,j}$ is the temperature, both at location i, j on a two-dimensional spatial grid.

Current climatic conditions were represented by 30-year (1981–2010) spatially interpolated climate normals from the PRISM Project (NACSE 2014). For future climate, we used an ensemble of climate models from the climate model inter-comparison project (CMIP-5) to assess future climate under different emission scenarios (RCPs), and to account for uncertainty in model projections due to variability among models. RCPs incorporate predictions of future greenhouse gas emissions and are numbered by their corresponding projection of radiative forcing at the year 2100. Under RCP 2.6, radiative forcing peaks at 3.0 W m^{-2} ca. year 2040 and declines to 2.6 W m^{-2} in year 2100. In RCPs 4.5, 6.0, and 8.5, radiative forcing stabilizes between year 2050 (RCP 4.5) and year 2250 (RCP 8.5).

For RCPs 2.6, 4.5, and 8.5, we obtained projections of year 2100 July daily maximum temperatures from five of the top-performing models for North America, according to evaluations by Watterson et al. (2014) (Table 1). RCP 6.0 was not evaluated because output from five of the top ten models could not be obtained from the NCCS THREDDS data service. The remaining models, however, yield useful projections as two extremes (optimistic: RCP 2.6, pessimistic: RCP 8.5) bracket an intermediate scenario (RCP 4.5). All data were obtained in raster format and assigned a common projection (UTM Zone 17N, datum WGS 1984). For each of these emissions scenarios, we obtained the mean, 5th percentile, and 95th percentile among the five selected models of July daily maximum temperature at each grid cell.

Region-wide suitability for red spruce in the Central Appalachians was estimated by combining (multiplying) the estimated probability of historical red spruce occurrence with the climatic suitability metric. This yields a combined regional suitability

Table 1 List of climate models used in ensemble projections of future climate

Scenarios	Model names	Ranks
RCP 2.6	MPI-ESM-LR	1
	HadGEM2-ES	3
	MRI-CGCM3	7
	GFDL-CM3.0	8
	CanESM2	9
RCP 4.5	MPI-ESM-LR	1
	HadGEM2-ES	3
	ACCESS1.0	4
	CNRM-CM5	5
	HadGEM2-CC	6
RCP 8.5	MPI-ESM-LR	1
	HadGEM2-ES	3
	ACCESS1.0	4
	CNRM-CM5	5
	HadGEM2-CC	6

Rank indicates the relative performance of the model at predicting climate over North America, as assessed by Watterson et al. (2014)

rating for 10 scenarios: current conditions, and the mean, lowest confidence interval, and highest confidence interval for each of three future climates (RCPs 2.6, 4.5, 8.5). The lowest confidence interval for suitability is created using the 95th percentile of projected July daily maximum temperature, since increasing exposure to high temperatures reduces suitability for red spruce. For each scenario, we map the distribution of combined suitability ratings and report the total area where the suitability rating exceeds 0.5 and 0.7. Additionally, we stratify our suitability index by latitude, elevation, and state to evaluate the relationship between each of these variables and suitability for red spruce, and to assess whether these relationships may change in future climates.

Mapping suitability in Weimer Run, WV

We also evaluate current and future suitability for red spruce in the Weimer Run Watershed, a 374 ha first-order watershed located in Tucker County, West Virginia (Fig. 1). The goal of this case study is to illustrate how our suitability projections can inform restoration planning, particularly in concert with local-scale information that can influence the efficacy of restoration efforts and may be unavailable or intractable over regional spatial extents. The Weimer Run Watershed is located within the Little Canaan Wildlife Management Area, property formerly held by the Canaan Valley Institute (CVI). In 1995, the property was acquired by CVI through NOAA. Previously, the property was owned by Dominion Power Company since the 1970s. In recent decades, *Rhododendron* coverage has increased steadily, primarily in large canopy gaps, along streams, and onto previously unoccupied southerly facing slopes (Atkins *unpublished data*). Greater *Rhododendron* coverage results in increased competition for light and resources within the forest that differentially places red spruce at a competitive disadvantage.

We assess changing suitability of Weimer Run Watershed for red spruce under different climate scenarios using the spatially averaged mean suitability value. At the spatial resolution of the climate projections, there is insubstantial spatial variability in our suitability index over the area of the watershed, and so we present a single value for each climate scenario to characterize how warming temperatures are likely to affect red spruce in this location. To address within-watershed spatial variability in site quality, we map two locally varying factors thought to affect the

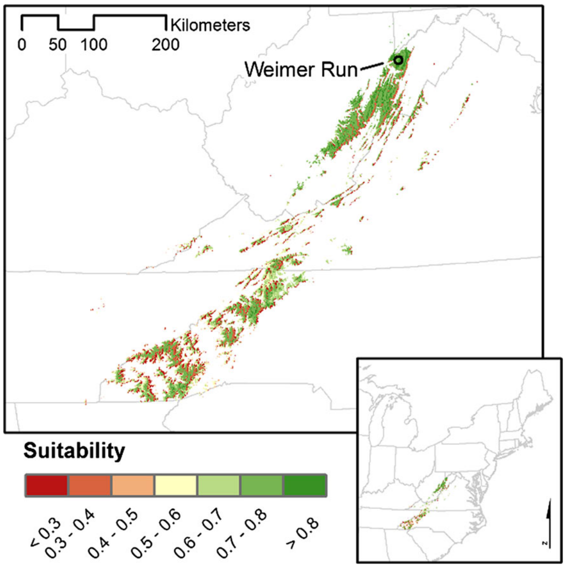

Fig. 1 Suitability for red spruce in the Central Appalachians under current climatic conditions

suitability and potential for restoration of red spruce: the current extent of red spruce within Weimer Run Watershed, and the extent and recent expansion of *Rhododendron* shrubs.

The current distribution of overstory red spruce may influence its future distribution because red spruce alters microhabitat soil conditions in ways that may enhance its competitive ability relative to other species (Dibble et al. 1999; Atkins *unpublished data*), thus reinforcing its potential success, and because existing, mature trees are a source of propagules. We mapped the extent of overstory red spruce based on interpretation of aerial orthoimagery in ArcGIS (ESRI, Redlands, California). A grid of 5 × 5 m cells was lain over 0.61 × 0.61 m pixel resolution images acquired on 10 March 2003 (USGS 2005). Each cell was classified as either containing red spruce or not based on visual interpretation of the aerial imagery and on investigator knowledge of the study area. Red spruce in the overstory can easily be distinguished from deciduous species by their greenness in winter, and can be separated from evergreen understory shrubs by their height and conical shape.

Over recent decades, the areal extent of understory evergreen shrubs in Weimer Run has increased by 33–54% from 1986 to 2011 based on spatial analysis of winter NDVI derived from snow-free Landsat TM scenes (Atkins *unpublished data*). Over the broader region, *Rhododendron* is expanding, ostensibly due to fire suppression (Phillips and Murdy 1985). We use maps from Atkins (*unpublished data*; see Online Resource 1 for description of methodology) to delineate the extent of *Rhododendron* in Weimer Run and interpret the potential for competition with red spruce based on areas where the estimated distributions of the two species overlap.

Results

Regional-scale suitability

At the regional level, ca. 14,000 km^2 were projected to be suitable for red spruce under current conditions (Table 2), far exceeding its current distribution. Under current conditions, summer temperatures may already constrain the range of red spruce relative to its historical range; however, many areas of low predicted suitability under current climatic conditions were at lower elevation or with southerly exposures and thus may be of marginal suitability for red spruce irrespective of ongoing climatic warming. Climate change may substantially restrict the potential distribution of this threatened species, even under optimistic emissions scenarios. Although under RCP 2.6, the confidence intervals suggested a small probability of the potential range of red spruce expanding (Table 2), the mean for RCP 2.6 indicated a likely 44.5% areal decline in sites with $s_{i,j} \geq 0.7$ and a 20.6% areal decline in sites with $s_{i,j} \geq 0.5$. Declines in suitability were greater under RCP 4.5, and under RCP 8.5 moderately to highly suitable sites began to disappear entirely from the landscape (Table 2). The confidence bounds on the area meeting our chosen suitability thresholds generally spanned two or more orders of magnitude, highlighting potential uncertainties in future climate and their impact on red spruce (Table 2).

Under all considered scenarios, losses of suitable red spruce habitat tended to occur at low latitude and low elevation, and under RCP 8.5 only the highest elevation sites were weakly suitable for red spruce (Figs. 2, 3). High elevation sites became increasingly important to red spruce as the severity of future climate warming increased from RCP 2.6 to 8.5 (Figs. 2, 3). Our approach predicts that, within our study region, red spruce is most likely to persist in the Allegheny Mountains of West Virginia, and may become extinct in more southerly portions of its present range, such as the Great Smoky Mountains (Figs. 2, 3). If the future climate is most similar to RCP 8.5, suitability for red spruce will be extremely low.

Suitability in Weimer Run, WV

Coherent with the pattern shown in our regional-scale analysis, year 2100 suitability for red spruce in Weimer Run Watershed is projected to decrease with increasing greenhouse gas emissions (Fig. 4). If greenhouse gas emissions remain high (RCP 8.5), this area, which currently supports red spruce, is predicted to become unsuitable for red spruce, but under a more optimistic reduced emissions scenario (RCP 2.6), the decline in suitability may be small. Even under moderate levels of greenhouse gas emissions (RCP 4.5), Weimer Run Watershed may continue to support red spruce (Fig. 4).

Table 2 Area (km^2) having medium ($\geq$0.5) and high ($\geq$0.7) suitability scores under current and projected future climatic conditions

	Suitability ≥ 0.5			Suitability ≥ 0.7		
Current	13,951.33			7691.42		
	LCI	Avg.	UCI	LCI	Avg.	UCI
RCP 2.6	4606.89	11,072.63	14,267.27	740.84	4267.87	12,708.76
RCP 4.5	271.25	3427.47	11,728.81	23.52	419.42	5567.68
RCP 8.5	0.00	9.41	1226.90	0.00	0.00	32.14

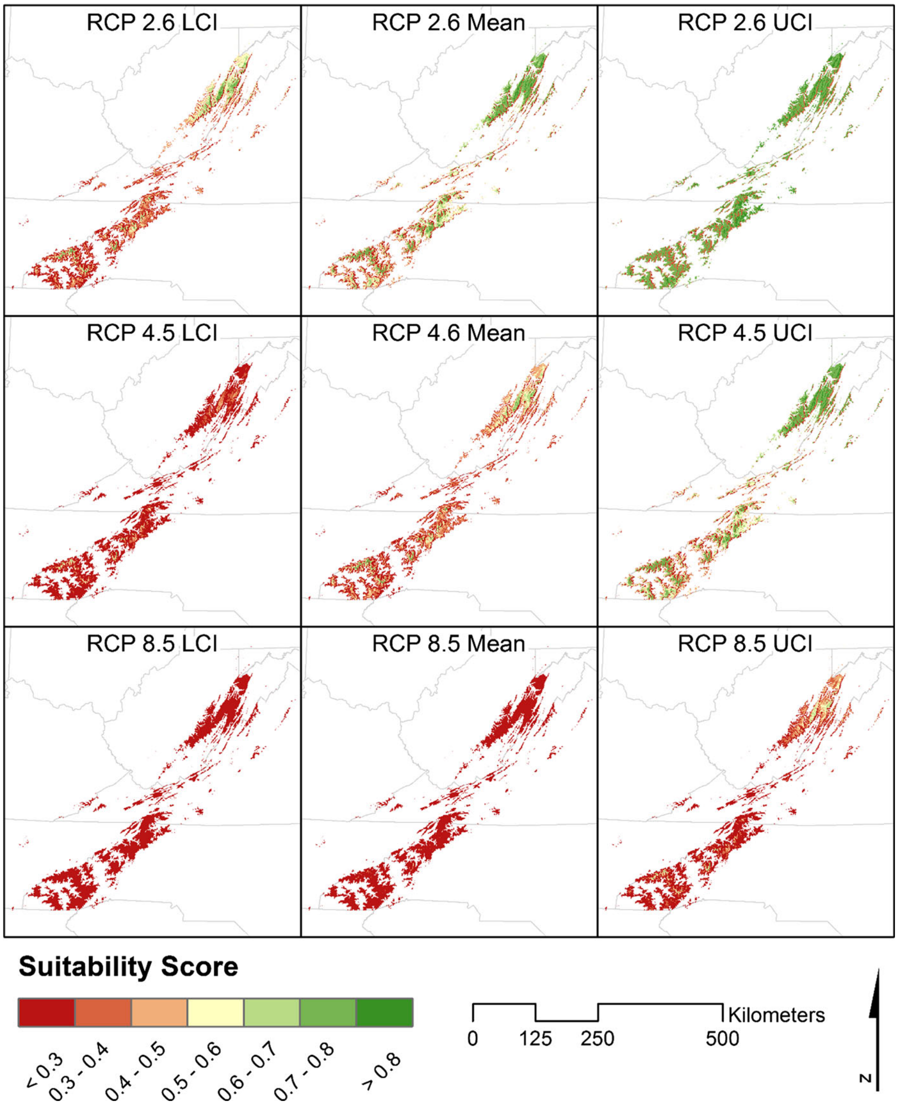

Fig. 2 Projected year 2100 suitability for red spruce in the Central Appalachians under three emission scenarios. Confidence bounds are obtained using the cell-wise 5th percentile (UCI) and 95th percentile (LCI) of predicted July mean daily maximum temperatures from an ensemble of downscaled climate projections

The present-day spatial distribution of red spruce within the watershed tended to mainly follow drainages and a riparian area (Fig. 5). *Rhododendron* tended to occur in the same areas, and is known to be expanding (Phillips and Murdy 1985; Atkins *unpublished data*). The close correspondence of red spruce with expanding understory shrubs suggests that *Rhododendron* and red spruce are in competition, to the potential detriment of red spruce in Weimer Run.

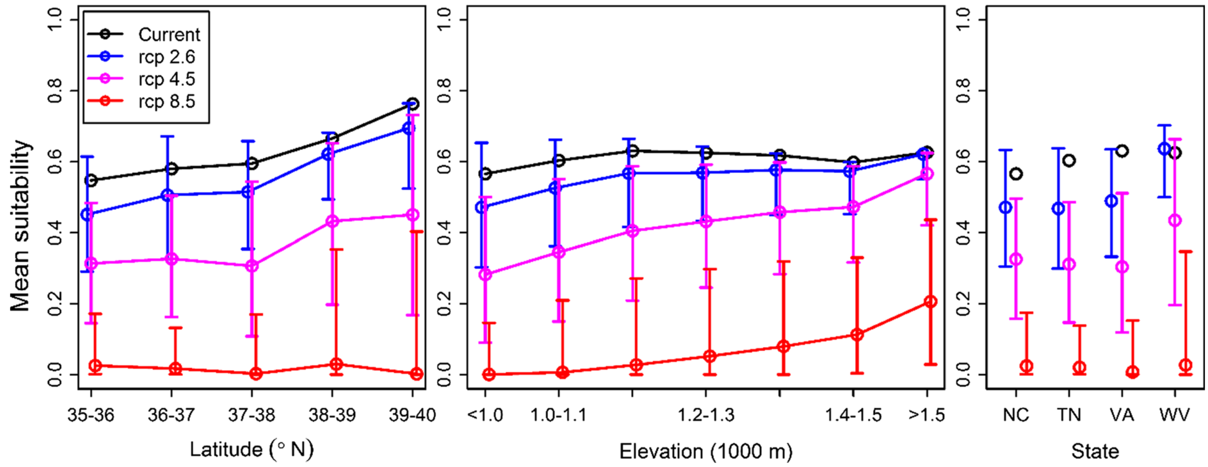

Fig. 3 Red spruce suitability under current and projected climatic conditions, stratified by latitude, elevation, and state. *Data points* represent the mean suitability index within the indicated range (*x*-axes) of the stratifying variable. For climate projections, *error bars* represent means for the upper and lower confidence intervals on July maximum temperature under each scenario

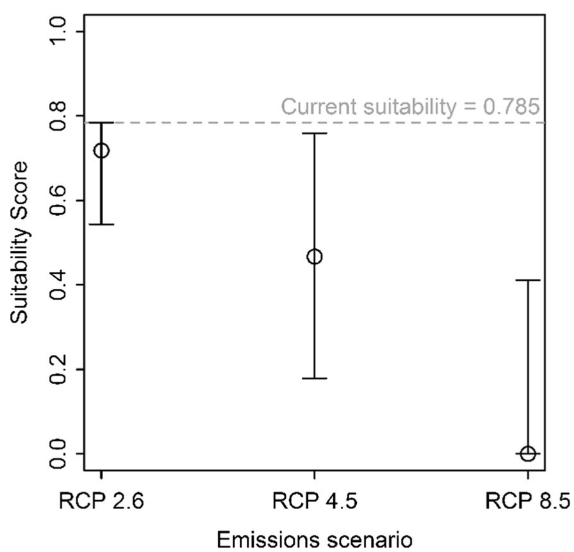

Fig. 4 Projected suitability of Weimer Run Watershed in year 2100 for three emission scenarios. The *dashed gray line* indicates the suitability score under current climatic conditions. Confidence bounds are obtained using the cell-wise 5th percentile (UCI) and 95th percentile (LCI) of predicted July mean daily maximum temperatures from an ensemble of downscaled climate projections

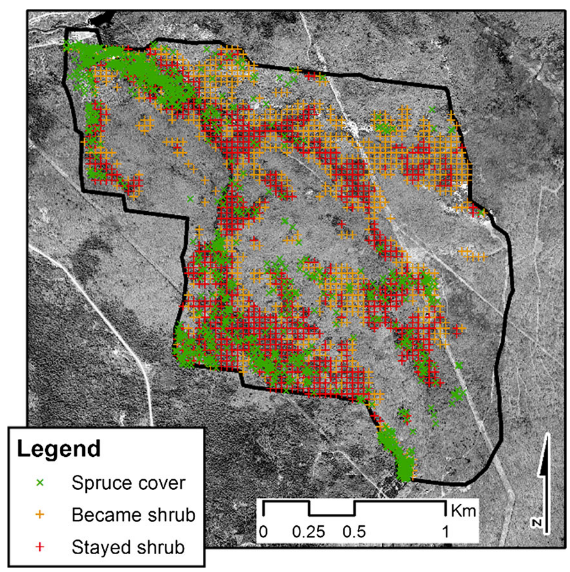

Fig. 5 Spatial distribution of red spruce and understory shrubs in Weimer Run Watershed. Spruce cover is estimated from interpretation of aerial photos from year 2003. Shrub extent and change therein is estimated from a 1986 to 2011 timeseries of Landsat5 TM images

Discussion

The ability of the Central Appalachians to support red spruce-dominated forests is likely to decline by 2100, but slowing climate change may enable this threatened species, and the rare flora and fauna associated with it, to persist. This broad message echoes other predictions (Koo et al. 2014, 2015; Beane and Rentch 2015). However, our findings may suggest greater hope for restoration efforts: under RCPs 2.6 and 4.5, the total area suitable for red spruce is likely to exceed its current extent of ca. 180 km^2 (Griffith and Widmann 2003; Brown and Vogt 2015) (Table 2). The geographic distribution of suitable sites is projected to change even under relatively optimistic scenarios (Figs. 1, 2, 3). While this general pattern is coherent with predicted effects of climate change on the range of this and other species (Parmesan and Yohe 2003), our application of an ensemble of downscaled climate projections permits high spatial resolution predictions of climate effects on red spruce, and enabled us to address uncertainty in climate projections, as represented by variability among models.

These findings imply that restoration efforts for red spruce would be enhanced by considering potential future climates to optimize allocation of often-limited resources. More specifically, predictions such as ours can be used in a top-down fashion to aid in identifying sites with strong restoration potential, i.e., those predicted to continue having climatic conditions supporting red spruce. Or in a more bottom-up fashion, one or more potential restoration sites can be vetted based on their predicted future suitability. Furthermore, suitability projections can be coupled with relevant local-scale data to further inform restoration potential. Toward that end, we evaluated the projected suitability for red spruce of Weimer Run Watershed in Tucker County, West Virginia and utilized available fine-resolution data on local conditions to show how such information can further guide restoration efforts. Because Weimer Run may become marginal red spruce habitat under RCP 4.5 and poor or entirely unsuitable habitat under RCP 8.5, it may not be the perfect target for restoration (Fig. 4). However, given that its suitability over all climate scenarios is relatively high compared to other parts of the region (Fig. 2), and that it currently supports red spruce (Fig. 5), restoring red spruce in Weimer Run Watershed has value and may have a reasonably high chance of success relative to other small watersheds in the region.

Within Weimer Run, potential restoration efforts should respond to local heterogeneity in environmental conditions. Although these are not the only local-scale factors influencing red spruce regeneration and restoration, we identified two locally varying factors thought to affect restoration efforts: the current distribution of red spruce, and the extent and expansion of understory shrubs (Fig. 5). Together, these factors have implications for where within the watershed to conduct restoration projects, and what treatments may be most effective. We observed red spruce and competitive understory shrubs both to be distributed mainly in moist drainages and riparian areas. Because shrubs like *Rhododendron* constrain understory red spruce via competition and altered nutrient cycling (Phillips and Murdy 1985; Clinton and Vose 1996), removal or thinning of the shrub layer may improve the health of extant red spruce. The creation of small to medium size canopy gaps through the removal of hardwood species that mimic the historical disturbance regime of the system (e.g., windthrow) may also release understory red spruce and improve restoration success probability (Rentch et al. 2016).

Moreover, planting red spruce in shrubby areas, or where shrub expansion is likely to occur, may be ineffective. Rather, plantings may be most successful near existing red spruce and where shrubs are sparse or absent. One such area in Weimer Run is located in the southernmost tip of the watershed (Fig. 5). In areas like this, red spruce should be exposed to less interspecific competition, and plantings may be supplemented by propagules from extant trees. Adequate numbers of red spruce seeds for regeneration disperse at least 100 m from the parent tree, showing a nearly flat response to distance of the proportion of dispersing seeds, but dispersal over longer distances may be rare (Randall 1974; Dumais and Prevost 2007). With respect to future climates, it is prudent to note that we do not explicitly address competitive interactions between red spruce and *Rhododendron*, including the potential for climate change to alter competitive balance. Altered interspecific interactions are an increasingly recognized impact of climate change (Post 2013). In this case, however, recent expansion of *Rhododendron* in Weimer Run is coincident with ongoing climate change, raising the possibility that *Rhododendron* is favored in a warmer, wetter climate. We also did not explicitly address potential climate-related range shifts in *Rhododendron*. Presently, co-occurrence of red spruce and *Rhododendron* is somewhat uncommon and mainly at low and mid elevations (Byers et al. 2010).

Given that a goal of this study was to predict the potential range of a currently rare species, we did not quantitatively validate the predictions of our model. Due to the constraints placed largely by logging and other human activities, the current distribution of red spruce is a poor indicator of its potential range. However, the model used to predict the historical extent of red spruce has been validated (Nauman et al.

2015), and our predictions correspond generally with maps of the red spruce range (e.g., West Virginia Department of Natural Resources 2013).

Future advances can refine the projections made by this study, and more closely link ecological mechanisms with the data underlying distribution projections. For example, foliar thermal stress and damage is in part a function of the duration of exposure to supraoptimal temperatures (Niinemets 2010). Hence, climate data at daily or finer time intervals could refine the relationship between rising temperatures and red spruce distributions. This may be increasingly important if climate change results in increases in the frequency and severity of extreme weather events. Such extreme events are also difficult to predict, particularly at fine spatiotemporal resolutions, and there may be uncertainty over mean climate patterns given difficulties of downscaling climate over complex terrain (Fridley 2009). Additional variables linked to red spruce health, such as cloud immersion (Berry and Smith 2012), could also be included in future studies provided they could be measured and projected over space.

Concern over the persistence of red spruce in the Central Appalachian mountains is supported by several studies (Iverson et al. 2008; Koo et al. 2015; Potter et al. 2010; Beane and Rentch 2015), including this one, predicting that climate change will make many parts of its distribution less hospitable. However, we also found that, under climate projections with somewhat optimistic assessments of our ability to curtail greenhouse gas emissions, it may be possible for red spruce to expand its range from its current distribution. Consequently, efforts to restore the species (e.g., Buckley 2014) may not be futile. The case of red spruce in the Central Appalachians is likely unique in that its current distribution has been so restricted by other anthropogenic changes that—even as climatic warming shrinks its potential range—its realized range, and abundance within it, potentially increase (Nowacki et al. 2010). However, a great deal of uncertainty remains, and even under optimistic climate projections the health of red spruce-dominated forests likely depends on well-executed restoration efforts that take into account large-scale factors such as climate change and local-scale factors including the competitive environment. This study illustrates an approach for such an effort based on multi-scale mapping using widely available data, which we propose could be applied to other areas being considered for restoration.

Acknowledgements T. Smith and two anonymous reviewers provided useful comments on an earlier version of this manuscript. This research was supported by the Department of Environmental Sciences at the University of Virginia. JAW was supported by USDA-NIFA 2015-03685.

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