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Managing Hardwood-Softwood Mixtures for Future Forests in Eastern North America: Assessing Suitability to Projected Climate Change

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Despite growing interest in management strategies for climate change adaptation, there are few methods for assessing the ability of stands to endure or adapt to projected future climates. We developed a means for assigning climate "Compatibility" and "Adaptability" scores to stands for assessing the suitability of tree species for projected climate scenarios. We used these scores to determine whether mixed hardwood-softwood stands or "mixedwoods" were better suited to projected future climates than pure hardwood or pure softwood stands. We also examined the quantity of aboveground carbon (C) sequestered in the overstory of these mixtures. In the four different mixedwood types that we examined, we found that *Pinus echinata-Quercus* mixtures in the Ozark Highlands had greater Compatibility scores than hardwood stands and greater Adaptability scores than pure *Pinus echinata* stands; however, these mixtures did not store more aboveground overstory C than pure stands. For *Pinus strobus-Quercus rubra*, *Picea-Abies*-hardwood, and *Tsuga canadensis*-hardwood mixtures, scores indicated that there were no advantages or disadvantages related to climate compatibility. Those mixtures generally had greater Adaptability scores than their pure softwood analogs but stored less aboveground overstory C. Despite the many benefits of maintaining mixedwoods, regenerating and/or recruiting the softwood component of these mixtures remains a persistent silvicultural challenge.

Keywords: hardwood-softwood mixtures, climate change adaptation, forest management, aboveground overstory carbon

"Mixedwoods" are stands containing hardwoods and softwoods. Although variations in the definition occur (e.g., Sauvageau 1995, Larouche et al. 2013, Leak et al. 2014), we use the term to describe stands in which neither component comprises more than approximately 75–80% of the composition (Helms 1998). In temperate forests of eastern North America, naturally occurring mixedwoods are found in the pine-oak (*Pinus-Quercus*), hemlock-hardwood (*Tsuga*-hardwood), and spruce-fir-hardwood (*Picea-Abies*-hardwood) types (Table 1; Figure 1). Mixedwoods can occur as isolated stands within hardwood- or softwood-dominated landscapes or they can comprise a large proportion of a forest landscape.

Mixedwood stands are often structurally complex and vertically stratified because individual species of hardwoods and softwoods have differing shade tolerances, growth rates, longevities, phenology, and crown and root structure (Kelty et al. 1992, Prévost 2008, Pretzsch 2014). Moreover, species within mixedwoods often employ differing regeneration and growth strategies. Because of this structural and compositional complexity (Kelty et al. 1992), there has long been interest in the benefits of mixed-

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Table 1. Summary of selected mixedwood types in eastern North America.

Mixedwood type	Hardwood component	Softwood component	Approximate Extent	Common disturbances	Stand structure
Shortleaf pine-oak	*Quercus alba, Quercus coccinea, Quercus falcata, Quercus rubra, Quercus stellata, Quercus velutina*	*Pinus echinata*	>1 million ha in Ozark and southern Appalachian regions on well-drained acidic soils	Frequent surface fire; historical and current logging; historical grazing; drought; minor wind and ice	Range from complex vertical structure to open woodlands with increasing fire frequency
Pitch pine-oak	*Quercus alba, Quercus coccinea, Quercus falcata, Quercus ilicifolia, Quercus rubra, Quercus stellata, Quercus velutina*	*Pinus rigida, Pinus echinata, Pinus pungens, Pinus virginiana*	>1 million ha in New England, Mid-Atlantic, and Appalachian regions and excessively well drained sandy soils	Frequent surface fire; historical logging; historical grazing; drought; minor wind and ice	Range from complex vertical structure to open woodlands with increasing fire frequency
White pine-red oak	*Quercus rubra, Quercus alba, Quercus velutina, Betula alleghaniensis, Betula lenta, Acer rubrum, Fraxinus americana*	*Pinus strobus, Tsuga canadensis*	0.5 million ha in New England on coarse-textured soils derived from granite and gneiss or residuum from sandstone and shale	Historical agricultural abandonment, logging, wind, and occasional surface fire	Two-storied, closed canopy stands with white pine occurring as emergent stratum over hardwood canopy
Spruce-fir-hardwoods	*Betula papyrifera, Betula alleghaniensis, Acer rubrum, Acer saccharum, Populus* spp., *Fagus grandifolia*	*Picea rubens, Abies balsamea, Picea glauca, Tsuga canadensis, Thuja occidentalis, Pinus strobus*	>10 million ha in the Northeastern United States, Quebec, and New Brunswick on shallow, rocky, or acid soils derived from glacial till	Historical and current logging, periodic spruce budworm outbreaks, hurricanes, minor wind and ice, rarely fire	Range from complex vertical and horizontal structure to single- or two-storied stands with few to many residuals over a dense canopy, depending on type and scale of disturbance
Hemlock-hardwoods	*Acer saccharum, Betula alleghaniensis, Betula papyrifera, Acer rubrum, Fraxinus americana, Fraxinus nigra, Ostrya virginiana, Prunus pensylvanica, Prunus serotina, Quercus rubra, Tilia americana*	*Tsuga canadensis, Abies balsamea, Picea glauca, Pinus strobus, Thuja occidentalis*	0.5 million ha in western Great Lakes, southeastern Canada, New England, and north central Appalachian regions on mesic sites with well-drained medium or coarse-textured soils	Infrequent, moderate-severity wind disturbance; historical logging; minor wind and ice	Complex vertical and horizontal structure

wood stands because of their potential to produce a greater timber volume or biomass (Waldrop 1989, Waskiewicz et al. 2013), to provide more diverse or unique habitats (Comeau 1996, Jung et al. 1999, Girard et al. 2004), and to be more resistant or resilient to contemporary insect outbreaks and diseases (Su et al. 1996, Campbell et al. 2008) than pure stands. Correspondingly, mixedwood stands may be well suited for achieving emerging management objectives related to climate change mitigation and/or adaptation (D'Amato et al. 2011, Gauthier et al. 2014).

Forests remove carbon dioxide from the atmosphere and convert it to biomass, thereby providing opportunities for mitigating future climate change through direct management of carbon dynamics (Dixon et al. 1994, Canadell and Raupach 2008). Previous studies have evaluated how forest management practices affect the rate of carbon accumulation (carbon sequestration) or the amount of carbon stored in live trees and deadwood (e.g., Hoover and Stout 2007, D'Amato et al. 2011). By integrating species with differing morphology and growth patterns, mixed-species stands can theoretically use growing space more completely than sin-

Management and Policy Implications

Forest management agencies are increasingly interested in establishing desired future conditions that are compatible with projected changes in climate. Maintaining, conserving, or restoring tree species diversity and enhancing carbon stocks are often identified as important climate mitigation strategies. Mixed hardwood-softwood stands or "mixedwoods" are often structurally and compositionally diverse because of the differing shade tolerances, growth rates, longevities, phenology, and crown and root structures of the constituent species. There has long been interest in the benefits of mixedwoods because of their potential to produce a greater timber volume or biomass, to provide more diverse habitats, and to be more resistant or resilient to contemporary pests and pathogens than pure stands. They also may be better suited for projected climates although assessing this has remained a challenge. We adapted a method for assessing the compatibility and adaptability of contemporary mixedwood stands to projected climate scenarios. Our assessment suggests that some mixedwoods are more compatible with projected future climates than are others but that all of the mixedwoods that we examined appeared to be better adapted than pure softwood stands.

Figure 1. Examples of mixedwood types in eastern North America. A. Shortleaf pine-oak forest in southern Missouri. (Courtesy of Missouri Department of Conservation.) B. White pine-red oak forest in southern Maine (Courtesy of Justin Waskiewicz.) C. Spruce-fir-hardwood forest in Quebec (Courtesy of Patricia Raymond.) D. Hemlock-hardwood forest in northern Wisconsin (Courtesy of USDA Forest Service.) Descriptions of associated species and common site types are provided in Table 1.

gle-species stands, resulting in greater productivity in mixed stands than in monocultures of any of the constituent species (Kelty et al. 1992, Pretzsch 2014). Commonly referred to as "overyielding," this phenomenon has been reported in spruce-beech (*Picea-Fagus*) mixtures in Europe (Pretzsch and Schütze 2009) and pine-oak mixtures in the northeastern United States (Waskiewicz et al. 2013). The potential for increased carbon storage in mixedwood stands suggests that these forests may be inherently favorable for climate change mitigation, although this generality has yet to be explored empirically.

There is growing interest in managing stands to be more compatible with and better adapted to anticipated climate conditions forecasted by various climate models (Gauthier et al. 2014). Proposed strategies include controlling stand structure by reducing stand densities or manipulating the spatial arrangement of trees (Linder 2000, McDowell et al. 2006, D'Amato et al. 2013) and managing stand composition by increasing species diversity or shifting composition to include those species better suited to projected climate scenarios (Thompson et al. 2009). The greater levels of compositional and structural diversity often associated with mixedwoods may represent forest conditions that are better able to sustain important ecosystem functions under the uncertain climates of the future than their pure hardwood or softwood analogs (Thompson et al. 2009). However, approaches for assessing the compatibility or adaptability of forests for projected climates in a meaningful and quantitative way have been lacking.

The recent advent of the Climate Change Tree Atlas[1] (see Iverson et al. 2008) and the series of *Vulnerability Assessment and Synthesis* reports (hereafter "Assessments") published by the US Department of Agriculture (USDA) Forest Service (for example, see Brandt et al. 2014, Handler et al. 2014, Janowiak et al. 2014, Butler et al. 2015) provides a means for quantifying tree species suitability to projected climate scenarios. The Climate Change Tree Atlas includes forecasted changes to the relative basal area and/or relative density of tree species by location. It also includes metrics related to the ability of individual tree species to survive and adapt to important drivers and stressors such as drought, insects and diseases, and fire. Information in the Climate Change Tree Atlas is summarized by region in the Assessments and is the culmination of more than a decade of research led by scientists from the USDA Forest Service working with university faculty and professional foresters and biologists from state and federal agencies (Iverson et al. 2011).

Scientists from the Northern Research Station of the USDA Forest Service, University of Missouri, University of Vermont, Ministry of Forests, Parks, and Wildlife in Quebec, and University of New Brunswick recently convened to examine the current state of knowledge of mixedwood forestry, with interest in resistance, resilience, and adaptability (for comprehensive definitions, see Thompson et al. 2009) to forcing agents such as insect and disease outbreaks and climate change, the potential for climate change mitigation, and the silvicultural challenges for mixedwood management. In this article, we present preliminary findings from an assessment of the compatibility and adaptability of mixedwoods to projected climate regimes using data sets from several common mixed hardwood-softwood forest types in eastern North America. Because increased carbon storage is often a forest management strategy for mitigating climate change, we also compared the aboveground overstory carbon estimates to determine whether hardwood-softwood mixtures stored more carbon than their pure hardwood or softwood analogs. Finally, we discuss some of the silvicultural challenges related to regeneration and recruitment of mixedwood stands.

Table 2. Data sets selected for the study included live trees >11 cm dbh from plots, stands, or experimental units from a number of long-term silviculture studies across eastern North America.

Mixedwood type	Location	Sample size and mean ± SE dbh (cm), TPHa, and BA (m^2 ha^{-1})	Constituent species
Shortleaf pine-oak	Sinkin Experimental Forest, Missouri, USA; Lat. 37.50° N, Long. 91.25° W	120 0.05-ha plots from 20 0.5-ha compartments measured (pretreatment) in 2009; dbh: 36.4 ± 0.3; TPHa: 169 ± 5; BA: 26.3 ± 0.6	*Quercus alba, Quercus velutina, Pinus echinata, Quercus coccinea, Quercus stellata, Carya* spp., *Acer rubrum*
White pine-red oak	Massabesic Experimental Forest, Maine, USA; Lat. 43.45° N, Long. 70.67° W	121 0.02-ha plots from six compartments unmanaged since 1947 and measured in 2007; subset of 62 plots having BA >20 m^2 ha^{-1} used for carbon calculations; subset dbh: 39.4 ± 1.4; TPHa: 286 ± 16; BA: 30.8 ± 1.4	*Quercus rubra, Pinus strobus, Acer rubrum, Quercus alba, Quercus velutina, Betula papyrifera, Tsuga canadensis, Pinus resinosa, Fagus grandifolia, Populus grandidentata, Betula lenta*
Spruce-fir-hardwoods	Penobscot Experimental Forest, Maine, USA; Lat. 44.85° N, Long. 68.62° W	54 0.08-ha plots from five compartments measured in 2009; subset of 20 0.08-ha plots from the unmanaged "reference" treatment having BA >20 m^2 ha^{-1} used for carbon calculation; subset dbh: 26.2 ± 1.2; TPHa: 618 ± 35; BA: 39.3 ± 2.9	*Tsuga canadensis, Abies balsamea, Acer rubrum, Pinus strobus, Picea rubens, Thuja occidentalis, Betula papyrifera, Populus tremuloides, Picea glauca, Populus grandidentata*
Hemlock-hardwoods	Seven sites in northern Michigan and Wisconsin, USA, including Chequamegon-Nicolet National Forest near Gilman, WI (Lat 45.16° N, Long 90.63° W), Argonne Experimental Forest, WI (Lat. 45.75° N, Long 88.96° W), Fox Maple Woods State Natural Area, WI (Lat 45.91° N, Long 88.46° W), Headwater Lakes State Natural Area, WI (Lat 45.97° N, Long 89.99° W), Kemp Natural Resources Station, WI (Lat 45.83° N, Long. 89.67° W), Patterson Hemlocks State Natural Area, WI (Lat 45.89° N, Long. 89.96° W), Sylvania Wilderness Area, MI (Lat 46.20° N, Long 89.28° W)	62 0.08-ha plots from seven separate sites measured in 2013; dbh: 32.8 ± 0.6; TPHa: 397 ± 13; BA: 39.8 ± 1.3	*Tsuga canadensis, Thuja occidentalis, Abies balsamea, Acer saccharum, Acer rubrum, Betula alleghaniensis, Tilia americana, Fraxinus americana, Quercus rubra, Prunus serotina, Betula papyrifera, Ostrya virginiana*

Lat., latitude; Long., longitude; TPHa, trees per hectare; BA, basal area.

Methods

Data Sets

To examine future climate compatibility and adaptability we compiled data for trees >11 cm dbh from four long-term, silvicultural studies conducted in USDA Forest Service Experimental Forests or on state lands located in different mixedwood types across eastern North America, including (1) shortleaf pine-oak (*Pinus echinata-Quercus*), (2) white pine-red oak (*Pinus strobus-Quercus rubra*), (3) spruce-fir-hardwood, and (4) hemlock-hardwood (Table 2). These data were selected because they included a wide range in the proportion of hardwoods and softwoods for each type. To examine the effect of increasing the softwood component on aboveground overstory tree carbon storage by trees, we restricted analysis to plots having an equivalent of full stocking (i.e., stand density ≥ B-level stocking) (*sensu* Gingrich 1967, Solomon et al. 1995). This ensured that differences in aboveground tree carbon could be attributed to the hardwood or softwood proportion and not confounded by inordinately low plot or stand density. Although simulated data could have been generated to ensure a broader range of :species, we used experimental data to examine the effects of actual mixtures where growing space allocation among species resulted from natural rather than modeled competition and stand development processes.

Climate Compatibility and Adaptability Scores

We calculated two metrics related to compatibility (Parallel Climate Model [PCM] B1 Compatibility and the Geophysical Fluid Dynamics Laboratory [GFDL] A1FI Compatibility) and one metric related to adaptability to projected changes in climate. The two Compatibility scores were derived from the future-to-current importance value ratios for individual species summarized by region in the Assessments (Brandt et al. 2014, Janowiak et al. 2014, 2017, Janowiak et al., in press). Importance values are an index of the relative tree species abundance within a forest community defined here as the weighted average of the relative basal area and relative density. Predicted future importance values for tree species have been modeled for different projected future climates and are available in the Climate Change Tree Atlas. The future-to-current importance value ratios have been used to indicate potential changes in the abundance of individual species under different climate models and scenarios. We used the future-to-current importance value ratios for two contrasting climate models and scenarios, the PCM B1 and the GFDL A1FI for the years 2070–2099. The PCM B1 and GFDL A1FI are well-documented models and scenarios for assessing the effects of climate change on trees because they provide the bounds for the extremes in projected temperature and precipitation. The PCM B1 is a low-emissions scenario modeled with the Parallel Climate Model projecting 0.7 to 1.5° C temperate increases and 50- to 74-mm precipitation increases throughout the study region in 2070 to 2099 compared with today. The GFDL A1FI is a high-emissions scenario modeled with the GFDL's model projecting 3.0 to 4.8° C temperature increases throughout the study region, a 79-mm precipitation de-

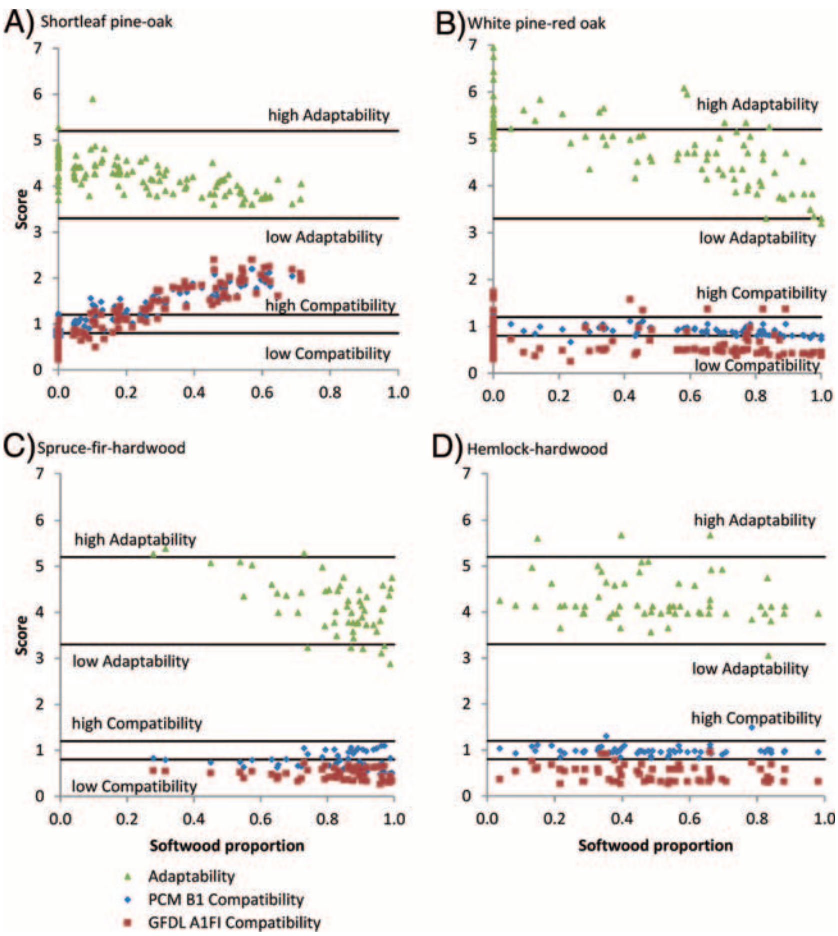

Figure 2. Projected climate Compatibility scores and Adaptability scores as a function of softwood proportion for shortleaf pine-oak (A), white pine-red oak (B), spruce-fir-hardwood (C), and hemlock-hardwood mixtures (D). Source data are listed in Table 2. Zones of high and low Compatibility and Adaptability are indicated.

crease at the shortleaf pine-oak study site in Missouri, and 3- to 5-mm precipitation increases for the other study sites during the same time period. We selected projections for the years 2070–2099 to quantify the compatibility within the lifespans typically expected for the tree species in the data sets. Greater detail about projected changes in precipitation and temperature can be found at the Climate Change Tree Atlas website.[1]

We extended the application of these ratios by calculating a single score for all of the species within the plots or stands of different hardwood-softwood mixtures and using this score as an index of the mixture's compatibility with future climates. To do this, we assigned the future-to-current importance value ratios for the PCM B1 2070–2099 and GFDL A1FI 2070–2099 projections for their respective regions to individual trees in each data set. We then calculated the average score for each plot or stand in the data set. In accordance with the guidelines in the Assessments, we categorized compatibility for each plot as low (scores <0.8), moderate (scores from 0.8 to 1.2), or high (scores >1.2). Low scores suggest that a given species mixture is expected to be less compatible under projected future climates, and high scores suggest that the species mixture is expected to be more compatible. Moderate scores indicate that little change in compatibility is expected.

The Adaptability scores that we used were described in detail by Mathews et al. (2011) as "modification factors" that provide additional information about how individual tree species respond to environmental change. Adaptability scores integrate both trait-related characteristics (such as shade tolerance, drought tolerance, and mechanisms related to regeneration and growth) and disturbance-related characteristics (such as tolerance to disease, insect pests, browse, drought, fire, and harvests). Adaptability scores are considered to be inherent characteristics of individual species that do not differ by ecoregion or under different climate change scenarios. Much as with the Compatibility scores, we also assigned species-specific Adaptability scores to each tree in our data and used the average score per plot or stand as a measure of the overall adaptive capacity of species mixtures. The Adaptability scores available in the Tree Atlas are scaled so that they range from 0 to 8.5. Following the guidelines included in the Assessments, plots or stands with Adaptability scores <3.3 indicate low adaptability, scores from 3.3 to 5.2 indicate moderate adaptability, and scores >5.2 indicate high adaptability.

We used the individual species adaptability scores reported in the Assessment for the Central Hardwood Region (Brandt et al. 2014) for the shortleaf pine-oak mixtures in the Ozark Highlands, scores reported for northern Wisconsin and western Upper Michigan (Janowiak et al. 2014) for the hemlock-northern hardwood mixtures, and scores developed for the northeastern United States for the white pine-red oak and the spruce-fir-hardwood mixtures (Janowiak et al., in preparation). By including a number of plots or stands, each with a range in the proportion of softwoods and hardwoods, the effect of increasing the softwood component on the two compatibility scores and the adaptability score could be determined.

Overstory Carbon (C) Calculations

We calculated the aboveground overstory C mass for each plot or stand using the biomass equation and parameters for different species groups presented by Jenkins et al. (2003) and assuming that the tree C mass was 50% of the tree biomass dry weight. We constructed general linear models of aboveground overstory C as a function of increasing softwood proportion using the GLIMMIX procedure (SAS version 9.3; SAS Institute, Cary, NC). Modeled values and 95% confidence intervals were plotted with actual data to illustrate trends.

Results

Shortleaf Pine-Oak

Data from the Sinkin Experimental Forest in Missouri showed that oak-dominated plots without shortleaf pine had Compatibility scores in the low to moderate range for the PCM B1 projections (score range 0.7–1.2) and for the GFDL A1FI projections (score range 0.2–0.9) (Figure 2A). Increasing the proportion of shortleaf pine basal area increased the Compatibility scores. High Compatibility scores occurred where the proportion of shortleaf pine ex-

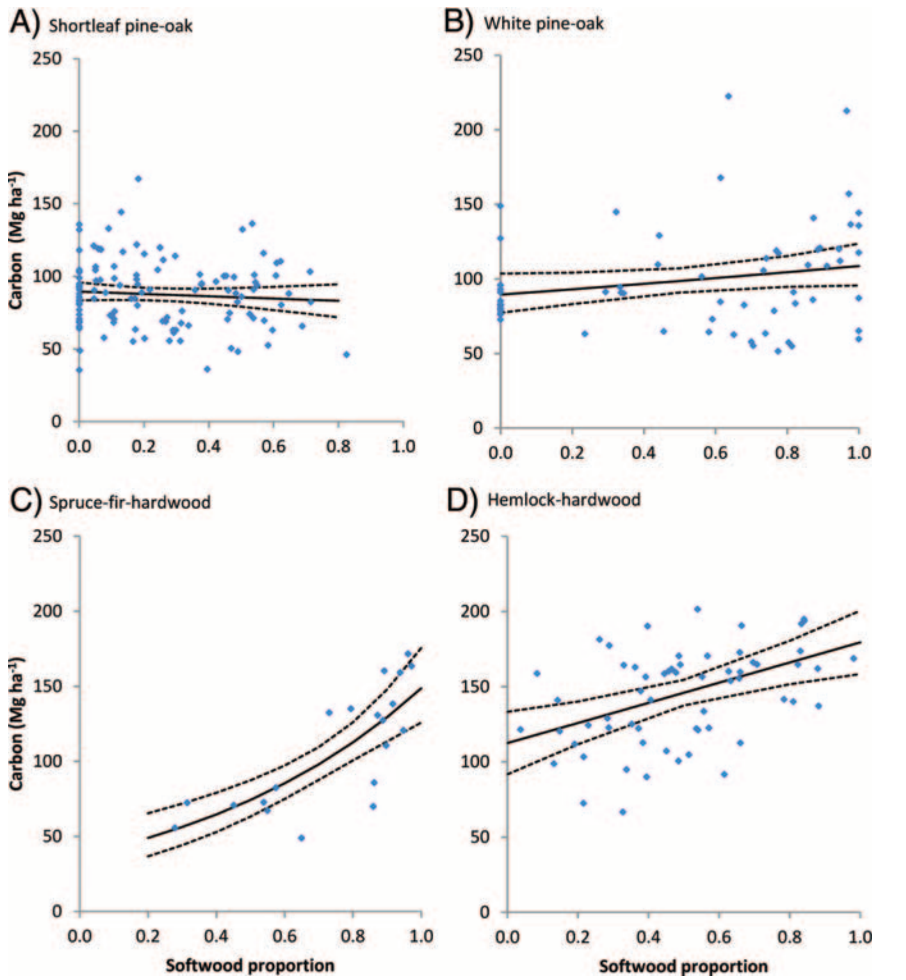

Figure 3. Overstory carbon as a function of softwood proportion for shortleaf pine-oak (A), white pine-red oak (B), spruce-fir-hardwood (C), and hemlock-hardwood mixtures (D). Source data are listed in Table 2.

ceeded 35% of the stand-level basal area for the PCM B1 projection and where the shortleaf pine basal area exceeded 32% for the GFDL A1FI projection. The Adaptability scores for mixed oak stands were moderate, ranging from 3.7 to 5.3. Increasing the proportion of shortleaf pine in mixed oak stands decreased the Adaptability score.

Oak-dominated plots had total aboveground overstory C of 89 Mg ha^{-1} (range, 36–136 Mg ha^{-1}). Increasing the proportion of shortleaf pine had no significant effect (P = 0.40) on the total aboveground overstory C (Figure 3A). Thus, shortleaf pine-oak mixtures appear not to store more aboveground overstory C than pure oak stands or pure shortleaf pine stands.

White Pine-Red Oak

Data from the Massabesic Experimental Forest in Maine showed that hardwood-dominated plots had Compatibility scores in the moderate range for the PCM B1 projections (score range, 0.7–1.3) and in the low to moderate range for the GFDL A1FI projection (score range, 0.3–1.7). Increasing the proportion of softwoods, which in this data set included primarily eastern white pine, generally had little effect on either the PCM B1 or the GFDL A1FI compatibility scores (Figure 2B). On average, the GFDL A1FI Compatibility scores were 30% less than the PCM B1 Compatibility scores regardless of the softwood proportion. The Adaptability scores were in the moderate to high range for the hardwoods only (score range, 5.0–8.0) and fell to the low range (score range, 3.0–4.0) as the softwood proportion approached 100% of the basal area. However, moderate Adaptability scores were maintained with mixtures of softwoods and hardwoods where the softwood component ranged from 20 to 80%.

Pure hardwood plots had aboveground overstory C of 90 Mg ha^{-1} (range, 63–148 Mg ha^{-1}). Increasing the proportion of softwoods marginally (P = 0.08) increased the aboveground overstory C (Figure 3B). Although there was considerable variation, aboveground overstory C appeared to increase linearly, and greater mass occurred, on average, in pure softwoods rather than in hardwoods or in hardwood-softwood mixtures.

Spruce-Fir-Hardwoods

Mixedwood stands in the Penobscot Experimental Forest in Maine had Compatibility scores in the low to moderate range for the PCM B1 projections (score range, 0.5–1.1) and in the low range for the GFDL A1FI projection (score range, 0.3–0.7). Increasing the proportion of softwoods, which in this data set included primarily eastern hemlock (*Tsuga canadensis*), balsam fir (*Abies balsamea*), white pine, red spruce (*Picea rubens*), and northern white-cedar (*Thuja occidentalis*), generally had little effect on either the PCM B1 or the GFDL A1FI compatibility scores (Figure 2C). On average, the GFDL A1FI Compatibility scores were 38% less than the PCM B1 Compatibility scores regardless of the softwood proportion. The Adaptability scores were moderate over a wide range of softwood proportions, but scores decreased to the low range where softwoods exceeded 90%.

For spruce-fir-hardwood mixtures, we estimated an aboveground overstory C of 71 Mg ha^{-1} (range, 20–172 Mg ha^{-1}) where hardwoods were dominant. Increasing the proportion of softwoods significantly increased ($P < 0.01$) the aboveground overstory C (Figure 3C). Although there was considerable variation, aboveground overstory C exhibited a curvilinear increase, and the greatest mass occurred, on average, in pure softwoods rather than in hardwood-softwood mixtures.

Hemlock-Hardwoods

Data from seven sites across northern Wisconsin showed that hardwood-dominated plots had Compatibility scores in the moderate range for the PCM B1 projections (score range, 0.8–1.5) and in the low to moderate range for the GFDL A1FI projection (score range, 0.3–1.0). Increasing the proportion of softwoods, which in this data set included eastern hemlock, northern white-cedar, balsam fir, and lesser amounts of white pine, generally had no effect on either the PCM B1 or the GFDL A1FI Compatibility scores (Figure 2D). On average, the GFDL A1FI Compatibility scores were 50% less than the PCM B1 Compatibility scores regardless of the softwood proportion. The Adaptability scores were in the moderate to high range (score range, 3.1–5.7) and were not affected by increasing the softwood proportion.

From these data we estimated that fully stocked hardwood stands had aboveground overstory C of 94 Mg ha^{-1} (range, 34–142 Mg ha^{-1}). Increasing the proportion of softwoods significantly increased ($P < 0.01$) the aboveground overstory C (Figure 3D). Although there was considerable variation, mass appeared to increase linearly and the greatest aboveground overstory C occurred, on average, in pure softwoods rather than in hardwoods or in hardwood-softwood mixtures.

Discussion

A range of compatibility, adaptability, and mitigation responses were observed across the mixedwood types examined in this study. There were, however, some commonalities related to geographic location. For example, the most southerly mixedwood type that we examined, oak-shortleaf pine, shows increased compatibility with future climates with an increasing softwood component, but no increases in aboveground overstory C. In northern mixedwood types, however, compatibility is unchanged by increasing the softwood component, but aboveground overstory C increases. Given these divergent responses, the following discussion will focus first on oak-shortleaf pine mixedwoods and then on the patterns observed in the northern types.

Shortleaf Pine-Oak

Our data suggest that shortleaf pine-oak mixtures in the Missouri Ozark Highlands are compatible with projected changes in climate for the region. Increasing the shortleaf pine component increased the Compatibility scores regardless of the climate projections we examined, and the greatest scores occurred with shortleaf pine-dominated mixtures (Figure 2A). However, the Adaptability scores decreased with increasing shortleaf pine proportion. The lower Adaptability scores with increasing shortleaf pine proportion were due to a number of factors. For example, shortleaf pine is intolerant of shade, which limits its ability to regenerate or recruit after partial canopy disturbances. It is also susceptible to insect pests (Brandt et al. 2014) such as the southern pine beetle (*Dendroctonus frontalis*) (Elliott et al. 2012). Others have reported that shortleaf pine is susceptible to annosum root disease caused by the fungi *Heterobasidion annosum* (Woodward et al. 1988), which is a particular problem in shortleaf pine-dominated stands and in plantations where root grafting among neighboring shortleaf pine trees allows the spread from tree to tree throughout the stand. The separation of individual shortleaf pine trees by hardwoods in mixed stands reduces root grafting of the pines and thus the spread of this disease. Overall, the Compatibility and Adaptability scores appeared to be optimum where shortleaf pine comprised about 50% of the basal area.

Managing for mixtures of shortleaf pines and oaks does not, however, appear to be a strategy for increasing aboveground overstory C (Figure 3A). It has long been demonstrated that pure shortleaf pine stands are capable of carrying a greater basal area or volume per hectare than oak stands (Brinkman and Smith 1968). This has been attributed to the smaller crowns and smaller growing-space requirements of shortleaf pine trees (see Rogers 1982). However, shortleaf pine wood density is also considerably less than that of oaks, and the lower wood density of this species (and therefore lower C per unit of wood volume) appears to negate any gains in aboveground overstory C that might otherwise be associated with the increased basal area or volume that can be carried in shortleaf pine-oak mixtures. Consequently, we found no evidence that shortleaf pine-oak mixtures have more aboveground overstory C than pure oak or pure shortleaf pine stands.

Silvicultural Considerations. Restoring and managing shortleaf pine and shortleaf pine-oak mixtures are priorities on public land throughout the southeastern United States (see Kabrick et al. 2007), such as on the Mark Twain National Forest and surrounding federal and state land in Missouri (Mark Twain National Forest Staff 2011). Regionwide conservation efforts include the Shortleaf Pine Initiative, which was organized in 2013 and began 6 years earlier as an initiative by the USDA Forest Service and the Southern Regional Extension Forestry to develop conservation plans for shortleaf pine ecosystems.[2] Our findings suggested that these efforts, which are aimed to restore the native biodiversity of these forests, are also highly compatible with strategies for managing for projected climate changes.

Despite the growing interest in restoring shortleaf pine-oak mixtures, past research has underscored the difficulty of recruiting shortleaf pine seedlings where oak and other competing hardwood reproduction is abundant (Table 3). Shortleaf pine seedlings are relatively shade intolerant and are initially slow growing. After a regeneration harvest, oaks and other hardwoods often will overtop shortleaf pine seedlings during the first or second growing season (Kabrick et al. 2015). Shortleaf pine eventually will succumb to hardwood competition after canopy closure of the regenerating cohort unless there are natural or human-caused disturbances to release the shortleaf pine (Blizzard et al. 2007). This problem is exacerbated with increasing site quality as greater soil water and nutrient supply favors the growth of the oaks and other hardwoods (Clabo and Clatterbuck 2015). Although it has been proposed that prescribed fire or mechanical methods can be used to release pine before, during, or shortly after canopy closure (Elliott et al. 2012, Kabrick et al. 2015), more research is needed about the type and timing of releases in shortleaf pine-oak mixtures.

White Pine-Red Oak, Spruce-Fir-Hardwood, and Hemlock-Hardwood

In the mixtures that commonly occur across north central and northeastern United States and southeastern Canada, increasing the softwood component had little or no effect on Compatibility scores (Figure 2B–D). This is because nearly all of the native tree species, hardwoods and softwoods, are projected to shift northward under the various climate change scenarios, with the greatest changes occurring under the GFDL A1FI projections (Iverson et al. 2008). Even though increasing the softwood component in the northern mixedwood types did not increase Compatibility scores, our analysis indicated that hardwood-softwood mixtures in this region are no less compatible with projected climates than pure hardwoods or pure softwoods. Therefore, if there are other compelling reasons for maintaining mixtures, such as esthetics, timber value, and diversity or the unique habitat that they provide, there is little evidence to suggest that compatibility with future climate will be reduced.

Higher Adaptability scores indicate that hardwood-softwood mixtures have an advantage over pure softwood stands in the northern region. This is largely because of

Table 3. Establishment and recruitment constraints and socioeconomic considerations (favorable or not) for regenerating or managing mixedwoods.

Mixedwood type	Establishment constraints	Recruitment constraints	Socioeconomic considerations
Shortleaf pine-oak	Limited suitable (mineral) seedbed for *Pinus echinata* seed germination due to absence of appropriate disturbances (Cooper 1989, Oswalt 2012); irregular (3–10 yr) *Pinus echinata* seed crop (Lawson 1990)	Intense hardwood competition during softwood recruitment (Zedaker et al. 1989, Lawson 1990)	*Pinus echinata* has lower economic value than do oaks in some locations reducing incentive to restore mixes
White pine-red oak	Limited suitable (mineral) seedbed for *Pinus strobus* seed germination due to absence of appropriate disturbances; midstory of *Tsuga canadensis* and other non-oak/pine species creates seedbed conditions (litter, light, and temperatures) unfavorable for *Pinus strobus* and *Quercus* spp. (Lorimer et al. 1994)	Intense hardwood competition during softwood recruitment, particularly on rich sites; lack of appropriate light conditions for maintaining advance regeneration of species prior to overstory disturbance	Predominant forest type across southern New England (forms matrix habitat across landscape); aesthetic value; watershed protection (Quabbin reservoir); *Pinus strobus* (in current condition—old field) has lower economic value than *Quercus* spp.
Spruce-fir-hardwoods	Limited suitable seedbeds for desired species (deadwood and exposed mineral soil); irregular seed crops for many species (*Picea rubens, Picea glauca, Pinus strobus, Thuja occidentalis*); heavy understory competition that expands quickly after canopy opening (Laflèche et al. 2000, Prévost et al. 2010)	Lack of light for survival of midtolerant species (*Betula alleghaniensis*, *Pinus strobus*); softwood seedlings grow more slowly than most hardwood associates; deer browsing puts additional pressure on developing regeneration (Larouche et al. 2010) and these interactions favor opportunistic species (e.g., *Acer rubrum, Betula papyrifera, Populus* spp.) and increase representation of hardwood species to the detriment of softwoods in managed stands	Forests have been repeatedly selectively harvested for desired species, resulting in undesirable species shifts; mixtures are easier to manage when there is a market for all commercial species; mixedwoods located near population centers in Quebec and Maine have high value for aesthetics and recreational activities such as hunting, fishing, camping, and hiking
Hemlock-hardwoods	Limited suitable seedbeds (deadwood or organic and mineral soil partially exposed by fire or treetip mixed); low seed viability; germinants vulnerable to drought (Godman and Lancaster 1990).	Slow growth; deer browse; thick, recalcitrant, forest floor; exotic pests.	*Tsuga canadensis* has lower economic value than dominant hardwood associates; favored by some landowners as "habitat" tree; susceptible to hemlock woolly adelgid in the East and potentially in the Lake States if future warmer climate allows pest to persist

the greater vulnerability of the softwood species in this region to drought and particularly to insect pests. For example, balsam fir, white spruce (*Picea glauca*), red spruce, and black spruce (*Picea mariana*) are susceptible to defoliation by the spruce budworm (*Choristoneura fumiferana*). Studies in New Brunswick have shown that defoliation over 5 or more years in typical outbreaks results in average mortality of 85% in mature fir and 40% in young fir and mature spruce stands (MacLean 1980, MacLean and Ostaff 1989). However, spruce-fir-hardwood mixtures experience less defoliation (Su et al. 1996), less growth reduction (Campbell et al. 2008), and less mortality (MacLean 1980, Bergeron et al. 1995) during outbreaks than pure softwoods. This is thought to result from more abundant or diverse parasitoid populations in mixed stands and/or greater small-larval dispersal losses in stands with nonhost species (Campbell et al. 2008). Optimum hardwood levels depend on outbreak severity (Needham et al. 1999, Sainte-Marie et al. 2015).

Under a warming climate, hemlock woolly adelgid (*Adelges tsugae*) and balsam woolly adelgid (*Adelges piceae*), both of which have historically been limited to more southern and coastal portions of their respective species' range, are expanding their ranges northward (Trotter et al. 2013). Yet our findings showed similar Adaptability scores among hemlock-dominated, mixed, and hardwood-dominated compositions (Figure 2D). Presently there is little evidence to suggest that hemlock trees in hemlock-hardwood mixtures are more vulnerable to the woolly adelgid than are trees in pure hemlock stands. However, it is generally recognized that pure hemlock stands are likely to become hemlock-hardwood mixes where the woolly adelgid is present (Ward et al. 2004). In addition, inventory data from the Forest Inventory and Analysis (FIA) program showed that hemlock has remained abundant in the landscape even where infestations have occurred (Trotter et al. 2013), suggesting that hemlock will not be entirely eliminated from infested stands. Instead, it is likely that hemlock will remain along with other hardwoods and softwoods in mixtures, albeit at a greatly reduced abundance.

Where storing C is an important objective, managing for white pine-red oak, spruce-fir-hardwood, or hemlock-hardwood mixtures appears to offer advantages over pure hardwood stands but not pure softwood stands (Figure 3B–D). Although we found no evidence of overyielding in mixtures, we did observe that C stored in overstory trees increased with an increasing proportion of softwoods. Increases were generally linear, suggesting that the pure softwood stands would store more C than mixtures or pure hardwood stands. However, given the other benefits and ecosystem services of mixtures, such as resilience to insect infestations discussed above, managing for mixed hardwood-softwood stands appears to strike a balance between managing for resistance and resilience and managing for C storage.

Silvicultural Considerations. There are silvicultural challenges associated with promoting and maintaining mixedwood stands in the white pine-red oak, spruce-fir-hardwood, and hemlock-hardwood types. For example, despite the prevalence of white pine-red oak forests on contemporary landscapes in southern New England, the anthropogenic origins of these forest types and their general successional trajectories make them particularly challenging to maintain in a mixed state on the landscape (Table 3). The maintenance of white pine in these mixedwoods presents the greatest challenge, given its inferior competitive ability relative to that of many of the hardwood species in these forests, particularly on more nutrient-rich sites (Goodlett 1960). Early silvicultural research in these systems recognized the importance of applying releases to cultivate large, advance white pine regeneration as a strategy to overcome this recruitment barrier (Cline and Lockard 1925). In addition, work examining the development of natural mixedwoods suggests that the establishment of white pine in groups served as a mechanism by which this species could ascend to canopy positions with pines on the periphery of groups serving to buffer the competitive effects of hardwoods on more centrally located pines (Hibbs 1982). This work has led to the application of patch selection approaches in attempts to recruit new white pine cohorts in white pine-oak mixedwoods (Kelty et al. 2003). However, long-term evaluations of the outcomes of these methods are lacking.

In spruce-fir-hardwood mixtures, the proportion of softwoods varies as a function of site and disturbance history (Seymour 1992). Some sites, e.g., those with well-drained, deep, moist soils on lower slope positions (Westveld 1930), naturally support mixedwoods. In such stands, silvicultural challenges include maintaining hardwood species of intermediate shade tolerance, such as yellow birch (*Betula alleghaniensis*), in stands dominated by more shade-tolerant softwoods and hardwoods (Prévost et al. 2010). Yet many contemporary spruce-fir-hardwood mixtures are the result of harvesting in softwood stands (i.e., spruce flats) that increased early successional and sprouting hardwoods to the disadvantage of slower-growing spruce (Westveld 1926, Bataineh et al. 2013) (Table 3). It can be difficult to maintain spruce in such stands, particularly if care is not taken to establish and protect advance regeneration before harvest. Red spruce, for example, produces seed less frequently, and the seeds are smaller and have a shorter period of viability than those of many of its competitors (Frank and Safford 1970). A lack of suitable seedbeds can also be limiting for red spruce, which prefers moisture-holding substrates such as decayed wood and mineral soil (Weaver et al. 2009). Hardwood leaf litter is a particularly poor microsite for red spruce regeneration, potentially further limiting seedling establishment as the hardwood proportion increases in mixedwood stands. In addition, although red spruce can establish and persist for many decades in shaded understory conditions, it is slow growing relative to competing species, even after release (Westveld 1926). Although there is no understory light level at which red spruce grows faster than its competitors (Moores et al. 2007), group selection or shelterwood cutting may create partially illuminated understories in which competition is minimized, physiological stress is reduced, and light is sufficient for growth of red spruce to match that of its competitors (Dumais and Prévost 2007, 2008, 2014). Given these challenges, research in spruce-fir-hardwoods is focused on identifying the stand conditions best suited to establishing and recruiting desired mixtures of hardwoods and softwoods and identifying how to achieve those conditions through silvicultural manipulation (e.g., Olson and Wagner 2010, Prévost et al. 2010, Saunders et al. 2014).

As with the other types, recruiting softwoods with hardwoods in hemlock-hardwood mixtures is also challenging (Table 3). For example, in the western Great Lakes region, hemlock regeneration favors decayed wood, specifically large hemlock boles, but this substrate is scarce because of past exploitive cutting of mature hemlock (Marx and Walters 2008). In addition, for most species of this mixedwood type, including sugar maple (*Acer saccharum*), recalcitrant understory layers of *Carex pensylvanica* (*sensu* Royo and Carson 2006) and exotic earthworms have created seedbed conditions that reduce natural recruitment (e.g., Powers and Nagel 2008). When saplings overcome these regeneration bottlenecks, small openings created by natural disturbances or by the selection system can release established trees to reach the canopy. Sugar maple and hemlock can persist and undergo multiple release cycles until reaching a dominant canopy position (Canham 1985, Webster and Lorimer 2005). Recent silvicultural research has been focused on alternative approaches to create regeneration sites (e.g., Fassnacht et al. 2015) and to accelerate release of understory with a range of canopy opening sizes (e.g., Kern et al. 2012).

Summary and Conclusions

We developed a method for evaluating the compatibility and adaptability of species mixtures to two projected climate scenarios by adapting information provided by the Climate Change Tree Atlas[1] summarized by region in the *Vulnerability Assessment and Synthesis* reports (Brandt et al. 2014, Handler et al. 2014, Janowiak et al. 2014, Butler et al. 2015). Numeric scores of species mixtures were calculated for current plot and stand data and used to assess the future compatibility and adaptability of various species mixtures to projected climate conditions for 2070 to 2099. We applied this method to evaluate the suitability of hardwood-softwood mixtures compared with that of their pure hardwood and pure softwood analogs. We also examined the aboveground overstory C of mixtures.

We found that shortleaf pine-oak mixtures are compatible with projected climate change. Mixtures that are approximately 50% shortleaf pine (basal area basis) appear to be optimum because this mixture balances Compatibility and Adaptability ratings. However shortleaf pine-oak mixtures do not store more aboveground overstory C than pure shortleaf pine or mixed oak stands. Findings suggest that managing for shortleaf pine-oak mixes ensures diverse forests compatible with contemporary restoration goals in the region and anticipated climates.

Among the three northern mixedwood types examined, there were fewer climate-related advantages compared with their pure hardwood or pure softwood analogs. Increasing the softwood or hardwood component had little effect on the Compatibility scores because the models projected that both the hardwoods and softwoods in the northern region would be less suited to future climates. These findings also suggest that there are no climate-related disadvantages of the mixtures. Thus, if there are compelling reasons for maintaining mixedwoods—because of their resistance and resilience to contemporary insect pests, habitat diversity, esthetics, or high timber value—our findings provide little evidence to suggest that their compositions should be shifted to hardwood or softwood dominance. In addition, mixtures generally had greater Adaptability scores than their pure softwood analogs because softwoods are generally more vulnerable to insect pests than are many hardwood species. Among the northern mixedwood types, the presence of softwoods generally increased aboveground overstory C.

Regardless of mixedwood type, the softwood component remains difficult to regenerate and/or recruit in the presence of hardwoods. A common and persistent research theme for regenerating and managing mixtures is ensuring softwood recruitment where desirable hardwoods are competing for growing space, particularly on highly productivity sites.

Endnotes

1. For more information, see www.nrs.fs.fed.us/atlas.
2. For more information, see www.shortleafpine.net/.

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