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Projected Tree Species Redistribution Under Climate Change: Implications for Ecosystem Vulnerability Across Protected Areas in the Eastern United States

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ABSTRACT

The degree to which tree species will shift in response to climate change is uncertain yet critical to understand for assessing ecosystem vulnerability. We analyze results from recent studies that model potential tree species habitat across the eastern United States during the coming century. Our goals were to quantify and spatially analyze habitat projections and their congruence under multiple climate scenarios and to assess the implications of habitat change for forest vulnerability and adaptation to climate change in and around protected areas. We assessed habitat projections of species habitat extent and forest composition for 35 tree species under climate change from 2000 to 2100 within National Park Service management units in the Appalachian Landscape Conservation Cooperative (ALCC), spanning an approximately 1,500 km latitudinal gradient. Our results show that forest composition and species ranges could change substantially under all greenhouse gas emissions scenarios and that model correspondence was stronger for projections of habitat declines than increases. Model correspondence generally increased at finer spatial scales, but varied by tree species and focal area. In the ALCC, forest composition was projected to change the most in protected area centered ecosystems (PACEs). Northeastern PACEs were projected to be suitable for tree species currently in southeastern PACEs, suggesting that intermediate suitable habitat regions could promote tree species persistence and mitigate the impacts of climate change on eastern forests. These results suggest that climate-specific management of eastern U.S. forest ecosystems will be critical but challenging, requiring integrated assessment and management of PACEs and protected areas as well as higher-resolution monitoring and modeling to inform

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spatially explicit management decisions within eastern U.S. parks.

Key words: species distribution modeling; species migration; forest management; conservation.

INTRODUCTION

Climate change is projected to catalyze the redistribution of tree species habitats across the eastern United States over the next 50–100 years (Currie 2001; Iverson and others 2004; McKenney and others 2011; Potter and others 2010). A rapid future temperature increase (~2–6°C/century in North America) is expected to cause northward shifts in suitable habitat that far exceed estimated historical migration rates for many species, including oak, spruce, and hemlock (~20–40 km/century; Bennett 1997; Davis and Shaw 2001; Parmesan and Yohe 2003; Iverson and others 2004; Davis and others 2005; Solomon and others 2007). Even the more conservative warming scenarios (for example, 1.8°C by 2100) are expected to exert considerable pressure on tree species to migrate tens to hundreds of kilometers to new climate space (Davis and Zabinski 1992; Solomon and others 2007). The consequent redistribution, adaptation, or local extirpation of tree species is expected to impact biodiversity, ecosystem function, ecosystem services, and human well-being (Peters and Myers 1991; Pimentel and others 1997; Hansen and others 2001; Matthews and others 2013). The impact of climate change on forest ecosystems, and consequently forest management, depends on a variety of intrinsic tree species characteristics (for example, phenotypic plasticity) and extrinsic environmental factors (Aitken and others 2008; Nicotra and others 2010). Mitigating these impacts is critically reliant on understanding changes in the distribution of tree species' bioclimatic ''suitable habitat'' conditions. Evaluating projected changes in the location and amount of suitable habitat provides the framework needed to evaluate tree species vulnerability to climate change.

A growing number of species distribution modeling (SDM) efforts have attempted to quantify the effects of climate change on the distribution of North American tree species and are frequently used to inform management responses (Araújo and others 2004; Iverson and others 2008a; McKenney and others 2011; Swanston and others 2011; Potter and others 2010; Brandt and others 2014; Handler and others 2014) to varying degrees of congruence (Elith and others 2006). Many studies employ empirical SDMs, which are based on correlative relationships between various environmental metrics (for example, temperature, precipitation, elevation) and observed species distributions (Franklin and others 2013). Our analysis focuses on tree species distributions modeled by two recent studies that employed empirical SDMs: Iverson and others (2008a) and McKenney and others (2011) (see ''Methods'' and ''Selection of Tree Species and Focal Area'' section). We selected these studies because they explored continental and sub-continental scale tree species redistribution using data from general circulation models (GCM) and greenhouse gas (GHG) emission scenarios that encompassed a range of climate forcings (that is, from low to high).

Iverson and others (2008a) used Random Forests (RFs) to project future tree species redistribution based on 36 predictor variables, including soil, climate, elevation, land use, and fragmentation. RF uses random subsets of data to construct a large number (that is, hundreds) of regression trees, grown to maximum size by the best split among a random subset of predictor variables at each node (Prasad and others 2006). These attributes—a large number of trees, maximal tree growth, and predictor variable randomization—result in minimal overfitting while upholding prediction strength and diversity among trees. McKenney and others (2011) used ANUCLIM (formerly BIOCLIM, Nix 1986; see also Booth and others 2014) to map tree species climate space, from which they projected potential future habitat distributions (McKenney and others 2006, 2007). ANUCLIM is one of the earliest generation climate envelope models and works by mapping the climate of the species observations (for example, average monthly temperature, precipitation) to the geographic locations of where that climate occurs (Franklin 2009; Booth and others 2014). Climate data are spatially interpolated from thousands of weather stations by elevation-dependent algorithms and bioclimatic variables. We note that Iverson and others (2008a) considered a combination of input variables (for example, climatic, edaphic, disturbance) whereas McKenney and others (2011) used climate variables only to project *potential* tree species habitat. Throughout the manuscript, we refer to current and future habitable regions as geographic projections of suitable ''habitat space''—the climatic and non-climatic component of the environmental conditions that support a species survival and growth (see also, Pearson and Dawson 2003). Our discussion of changes in tree species extent and forest composition necessarily refers to the occurrence of habitat space.

Our objectives were to assess the congruence and divergence of tree species responses to climate change for projections from Iverson and others (2008a) and McKenney and others (2011) (that is, correspondence of habitat space in 2100), and to quantify changes in the amount and distribution of tree species suitable habitat. We evaluated projections under a range of warming scenarios across four land management domains: the eastern U.S., the Appalachian Landscape Conservation Cooperative (ALCC), National Park Service (NPS) units within the ALCC, and Protected Area Centered Ecosystems (PACEs) around NPS units. We assume that areas of correspondence between the two efforts are likely to have higher probability of future change or stability.

We characterize our analyses across these focal areas within a comprehensive vulnerability assessment framework (Glick and others 2011) useful for evaluating the vulnerability of ecosystems and species to climate and land-use change in conservation areas across North America. We hypothesize that (1) correspondence will be greater under low emissions scenarios, as the differences between projections will be amplified by higher temperatures under high GHG emissions; (2) species with larger extents (that is, greater occurrence in a focal area) will show more congruent responses to climate as compared to species with smaller extents (especially those with strong edaphic controls); (3) correspondence will decrease at finer spatial scales as climatic drivers of distributions give way to more local controls (topography, disturbance, soils; (4) Iverson's models where elevation was among the top predictor variables will be less congruent with models from McKenney's group, as elevation was not a direct predictor variable but rather used to downscale climate station data.

The remainder of this paper explores why and when we might expect congruent (or divergent) responses of tree species to climate change; evaluates projected redistribution of eastern tree species in light of these expectations; and discusses how these results might affect forest management in our focal protected areas across the eastern United States. We first detail the methods used to select focal tree species, process geospatial data, and compare suitable habitat distributions. We then present results evaluating the correspondence between habitat projections and the extent and location of future habitat space. Lastly, we discuss tree species redistribution patterns, factors influencing tree species redistribution and model correspondence, and implications of these results for ecosystem vulnerability and adaptation to climate change in conservation and protected areas across the eastern U.S. We expect this study to improve understanding of future climate-ecosystem interactions in the eastern U.S., thus informing assessments of ecological vulnerability to climate change and supporting efforts to mitigate the ecological impacts of climate change.

METHODS

Selection of Tree Species and Focal Areas

We extracted tree species habitat projections across (1) the eastern U.S., to contextualize broad-scale projections of forest redistribution and compositional change across land management units operating at different scales, including (2) the ALCC, a collaborative (public–private) conservation unit rooted in scientific research and best practices to ensure the sustainability of its environmental resources (http://www.doi.gov/lcc/index.com); (3) NPS units within the ALCC; (4) PACEs, the geographical aggregate of a protected area (that is, NPS unit) and the zone around the protected area in which human activities could influence ecosystem processes and viability (Hansen and others 2011). We focused on four of the approximately 30 NPS units in the ALCC, spanning a broad latitudinal gradient: Great Smoky Mountains National Park (GRSM), Shenandoah National Recreation Area (SHEN), Delaware Water Gap (DEWA), and Upper Delaware Scenic and Recreational River (UPDE). We aggregated DEWA and UPDE NPS units for analysis because of their proximity and the resolution of the geospatial data, and we collectively refer to them as ''DEWA''.

The geospatial data we considered encompass a diversity of tree species and a range of climate change scenarios (for example, exposure; Glick and others 2011). We selected a subset of 35 tree species from Iverson and others (2008a) and McKenney and others (2011) that are projected to have considerable future range reduction or expansion (Appendix A in supplementary material). These species are also biologically or economically important (for example, longleaf pine, and sugar maple), or threatened by disease or invasive pests (for example, balsam fir), although disease and pest impacts were not modeled by Iverson and others

(2008a) and McKenney and others (2011). This subset of tree species could thus be most impacted by climate change (that is, high sensitivity; Glick and others 2011). For this subset, we considered redistribution projections under all GCMs and emissions scenarios reported by Iverson and others (2008a) and McKenney and others (2011), totaling to six GCMs and three emissions scenarios (Table 1). For all analyses, we aggregated high and low emissions into ''ensemble high GHG emissions'' and ''ensemble low GHG emissions'' projections. Tree species redistribution metrics in this study relate to fundamental vulnerability components such as *exposure*, which expresses the degree of change that a species or system is projected to experience, and *sensitivity*, which is the degree to which a system is likely to be affected by or responsive to climate change (Glick and others 2011). Combined, exposure and sensitivity describe the potential impact of future GHG emissions on tree species ranges.

We evaluated the potential impact of climate change on tree species by assessing habitat models that were trained with ecophysiological niche properties, representing sensitivity, and run with GCMs representing a range of climate forcings, representing exposure. Datasets of current and future suitable habitat space for tree species were provided by the United States Forest Service and Canadian Forest Service. Shapefiles were re-projected to a common coordinate system (the North American Datum of 1983), gridded, and, in the case of Iverson's abundance estimates, recoded as present based on an ''importance value'' threshold greater than 0.05 (see Iverson and others 2008a).

Metrics of Tree Species Response to Climate Change

We measured the range of tree species habitat redistribution under all climate scenarios through three metrics: (1) change in suitable habitat space; (2) change in the center of spatial distribution; and (3) changes in forest habitat composition (within and between protected areas) (Table 2). The metrics we use broadly characterize processes important to forest ecosystems and thus ecological vulnerability to climate change, yet these processes are not considered in the models by Iverson and others (2008a) or McKenney and others (2011). For instance, change in habitat space relates to ecological factors including interspecific competition (that is, where habitat space overlaps); change in mean center relates to migration potential, an area of active research (for example, Iverson and others 2004); Jaccard distance relates to changes in forest composition and relative changes in biodiversity; the two correspondence metrics are means to assess the congruence or divergence of tree species response to climate for the first three metrics.

Suitable habitat space change (ΔSHS) was expressed as the ratio of future to current occurrence (that is, number of ''presence'' grid cells) in suitable habitat (Iverson and others 2008a). We calculated ΔSHS for all tree species under all climate scenarios (the 12 GCM/GHG emissions scenario pairs) across the focal areas (eastern U.S., ALCC, PACE, NPS). Statistical operations were conducted using the R software package (R Core Team 2013).

Shift in geographic mean center (ΔMC) was expressed as the shift in the center of a tree species extent across the eastern U.S. (Iverson and others 2008a) and calculated using the *Generate Near Table* tool in ArcGIS, which calculates the distance and direction between two features. We created current and future geographic mean center features (points) for each species by separately stacking low and high GHG emissions grids (with the *Cell Statistics* tool), converting the stacked grids to point features, and calculating the mean center weighted by the point values.

Table 1. General Circulation Models (GCMs) and Emission Scenarios Considered in the Focal Studies, and the Projected Temperature Increases Associated with Each Emissions Scenario

Author	General Circulation Models (GCMs)	Emissions scenario[a]	Temp (°C)[b]
Iverson and others (2008a)	PCM, GFDL CM2.1, HadleyCM3	A1FI	5.3
		B1	2.6
McKenney and others (2011)	CCSM3.0, CSIRO-Mk3.5, CGCM3.1	A2	4.5
		B1	2.6

Emission scenarios provide projections of the amount and timing of CO_2 emissions under different assumptions of future economic growth. Changing CO_2 concentrations are key drivers of GCMs, which model physical processes like oceanic and atmospheric circulation, and provide gridded projections of temperature and precipitation.

[a] *A1FI emissions scenario represents an economically driven, globalized future with intensive fossil fuel consumption. A2 represents a future defined by regionally driven economic development. B1 represents an environmentally friendly, regionalized future that is relatively more ecologically friendly (from Nakicenovic and others 2000).*

[b] *Mean temperature increase in the eastern U.S. (east of 100th meridian) by 2100 relative to 2000, based on data from Iverson and others (2008a) and McKenney and others (2011).*

Jaccard distance measures compositional similarity between two sites or at the same site at different points in time (Jaccard 1912). We calculated Jaccard distance from the species grids from each modeling effort to compare similarity in current and future forest composition both within and between protected areas. In the former, we calculated Jaccard distance within each focal area (for example, ALCC) as the per-grid cell intersection ($\cap$) of unique species divided by their union ($\cup$), under current (A) and future (B) distributions for each author (that is, $1 - [A \cap B / A \cup B]$; for example, whereby B is the ensemble average for projections under the A1FI GHG emissions scenarios). We similarly derived Jaccard distance to compare forest composition between PACEs. This inter-PACE Jaccard distance compared the potential future forest composition of one PACE with the current of another.

Assessment of Model Correspondence

We assessed the correspondence between (1) projections of individual species habitats and (2) Jaccard distance maps (correlation) (Table 2). We calculated GCM correspondence (that is, spatial correspondence between pairs of suitable habitat grids) for each species across the eastern U.S., the ALCC, and its associated PACEs. For each species, GCM correspondence was calculated for all unique pairings of GCMs (between authors) by dividing the number of co-located grid cells by their union in the focal area. The resulting GCM correspondence metric quantified the spatial correspondence between pairs of GCM projections. GCM correspondence was calculated separately for low and high emissions, resulting in a range of nine correspondence values for each species (for example, high GHG emissions pair: HadleyCM3 [A1FI] and CGCM3.1 [A2]; Table 1). We mapped GCM correspondence by summing tree species grids under high and low GHG emissions (stacks of six grids; one grid per GCM/emissions scenario combination), resulting in two future maps per species. We compared the correspondence maps with their corresponding current modeled distribution, represented by the union of the current extent from Iverson and others (2008a) and McKenney and others (2011).

We investigated, on a species by species basis, the relationship between the occurrence of suitable habitat and GCM correspondence in the eastern

Table 2. Summary of Analytical Metrics

Metric	Abbr.	Definition	Analytical application	Example	Reference
Shift in geographic mean center	ΔMC	Distance (km) from current to future mean center of species extent	*Redistribution* Evaluate projected shifts in species extent (distance and direction)	Appendix A in supplementary material	Iverson and others (2008a)
Suitable habitat space change	ΔSHS	Ratio[a] of future to current occurrence in suitable habitat space	*Redistribution* Measure change in species habitat occurrence, relative to current	Table 4, Appendix D in supplementary material	Iverson and others (2008a)
Jaccard distance	–	Compositional dissimilarity[b] between two sites (e.g. grid cell, protected area) or at same site at different times	*Redistribution* Evaluate changes in forest habitat composition	Figure 4, Appendix E in supplementary material	Jaccard (1912)
GCM correspondence	–	Percent of overlapping grid cells between pairs of GCM projections under the same emissions scenario	*Correspondence* Measure the spatial agreement between suitable habitat projections	Figures 1, 2, 3, Table 3, Appendix B, C in supplementary material	n/a
Jaccard distance correlation	–	Correspondence between projected changes in forest composition	*Correspondence* Assess spatial/statistical agreement for forest habitat composition change	Figure 4C, E	n/a

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[a] *ΔSHS = occurrence (2100)/occurrence (current), $\Delta SHS > 1$ represents increase, $\Delta SHS = 0$ represents stability, $\Delta SHS < 1$ represents decrease.*

[b] *Jaccard = $1 - ([A \cap B/A \cup B])$; *A = current extent of occurrence, B = future extent of occurrence; $\cap$ = intersection of unique species; $\cup$ = union.*

U.S., ALCC, and PACEs to assess whether species occurrence in a focal area influenced the spatial agreement and average correspondence between GCM projections. For low and high GHG emissions scenarios, we correlated (Pearson coefficient) the average GCM correspondence (that is, average of all nine values for each species) with occurrence of suitable habitat, calculated as the percent of grid cells in the focal area in which a species habitat was present (separately under ensemble high and low GHG emissions). The correlation between average GCM correspondence and species occurrence for each focal area was calculated using only the species present under all six GCMs. Consequently, the number of observations in the correlations ranged from 30–35, depending on the focal area. For each focal area, we calculated the average correspondence (separately under high and low GHG emissions) for the subsets of tree species occurring across at least 75% of the focal area and those occurring across 25% or less of the focal area. We also calculated average correspondence for the subsets of tree species where elevation-related predictor variables ranked within or outside of the top five predictors of tree species habitat space in the eastern U.S. (by Iverson and others 2008a).

We assessed the correspondence between Jaccard distance maps (that is, projected changes in forest composition) by calculating the spatial correlation between them. We first resampled distance maps calculated using data from McKenney and others (2011) to 20 km (using bilinear interpolation). We then applied a moving window (5 × 5-grid cell window size) to Jaccard distance rasters from both Iverson and others (2008a) and McKenney and others (2011) and extracted statistics (Jaccard distance, correlation) to assess the response of forests to climate change within the context of protected areas.

RESULTS

Correspondence Between Tree Species Redistribution Projections

The correspondence between projections of species habitats in 2100 under ensemble low GHG emissions was generally higher (average correspondence ~61%, across all tree species) and less variable than projections under ensemble high GHG emissions (Figure 1; Table 3). The greatest difference in correspondence was at the eastern U.S. scale, where model congruence was 50% under low GHG emissions and 40% under high GHG emissions (on average; Table 3). Correspondence was also greater under low GHG emissions when averaged across all PACEs, yet variable by PACE and greater under high GHG emissions in the SHEN PACE.

There was a distinct spatial trend, whereby model correspondence generally increased at finer spatial scales from about 45% in the eastern U.S. to approximately 65% (on average) in PACEs (Table 3). Correspondence was higher for more frequently occurring species (≥75% occurrence in the focal area), but varied by species and focal area (Appendix B in supplementary material). For more frequently occurring species, the dominant predictor variables (that is, highest importance score from Iverson and others 2008a, b) correlated with correspondence were precipitation and soil (for example, mean growing season precipitation, potential soil productivity, and soil slope of a soil component). For less frequently occurring species (≤25% occurrence in the PACE), correspondence was 3–6% (on average), and temperature and soil variables ranked most frequently as the most important predictors of habitat (for example, mean growing season temperature and soil pH). The influence of elevation-related predictor variables on model congruence was minimal (Appendix C in supplementary material).

The strongest correspondence between GCM projections generally occurred in northern regions of species' projected extents (for example, balsam fir and sugar maple, Figure 2). There were moderate to strong positive correlations between species habitat occurrence and GCM correspondence (Pearson correlation coefficient $r = 0.90$ and 0.86 under high and low GHG emissions in the ALCC, respectively) (Figure 3). There was a clear latitudinal gradient within the ALCC, whereby the correlation between model correspondence and species occurrence was lower in more northerly PACEs.

Tree Species Habitat Redistribution Projections

The magnitude of individual tree species habitat shifts across the eastern U.S. was highly variable, owing to the diversity of tree species and climate scenarios considered, yet collectively greater under high emission scenarios than low emissions (average ΔMC 342 vs. 199 km, respectively; Appendix A in supplementary material). The range of projected change was also generally wider under high emissions climate scenarios (that is, A1FI, A2) and much larger for species that were expected to increase in the ALCC (median change in habitat

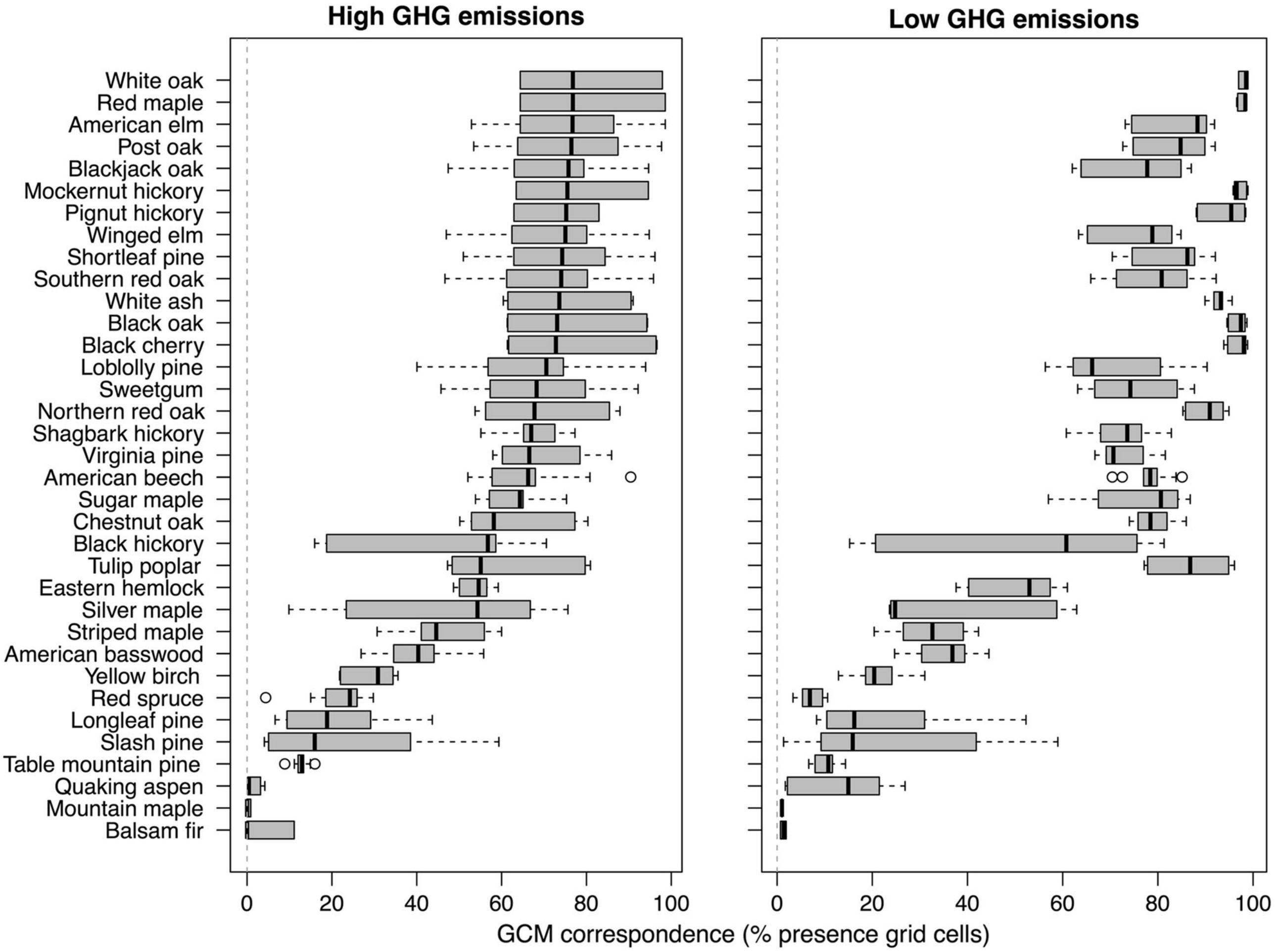

Figure 1. Boxplots of correspondence values for all unique pairwise GCM combinations (Table 1) for projections of individual species distributions under ensemble high (A1FI, A2) and low (B1) GHG emissions scenarios by 2100. Each species boxplot has nine observations. Correspondence values were calculated as described in Assessment of model correspondence section. GHG = greenhouse gas emissions, GCM = general circulation model.

space, for example, black hickory; Appendix D in supplementary material). More species were projected to lose habitat space in the ALCC under average high emissions (A1FI, A2) than under average low emissions (B1) (46% of species vs. 43%, respectively, based on median ΔSHS). The tree species projected to lose the most habitat space in the ALCC under ensemble average emissions were balsam fir, quaking aspen, and red spruce, whereas the greatest gainers included black hickory, slash pine, and southern red oak (Table 4). Of the different management unit types, the greatest changes in tree species habitat space occurred in PACEs (Table 4) and more species were projected to lose habitat space in GRSM PACE than the other PACEs. Under ensemble average emissions, the species projected to lose the most habitat space in PACE and NPS units were balsam fir, quaking aspen, and red spruce, whereas the species projected to gain the most included slash pine, post oak, and southern red oak (Table 4).

Projected Changes in Forest Habitat Composition

Forest habitat composition was projected to change most in northern PACEs (Jaccard distance = 0.48, 0.39, 0.34 for the DEWA, SHEN, and GRSM PACE, respectively) and NPS units (0.49, 0.42, 0.41) under high GHG emissions scenarios, and was variable by protected area and between studies (Figure 4). Furthermore, the correlation between Jaccard distance values was positive under ensemble high GHG emissions scenarios (except for SHEN PACE and NPS unit, and GRSM PACE), albeit weak ($r < 0.2$ for all focal areas), and generally strengthened with decreasing spatial extent. The

Table 3. Average GCM Correspondence Values by Species, Under Ensemble Average High and Low GHG Emissions, for the Eastern U.S., ALCC, and PACEs

Species	Eastern U.S.	ALCC	DEWA PACE	SHEN PACE	GRSM PACE
High GHG emissions					
Sugar maple	56.9	62.8	72.1	61.4	20.2
Northern red oak	56.5	69.7	83.8	80.6	33.5
White ash	55.9	75.0	69.4	100.0	79.2
Black oak	55.3	76.3	75.7	100.0	62.2
Shagbark hickory	53.5	67.6	97.3	68.5	64.2
White oak	53.4	79.7	97.3	100.0	70.8
American elm	53.2	76.0	97.3	100.0	47.5
Black cherry	52.1	77.0	97.3	100.0	63.8
American beech	50.9	67.3	97.3	75.3	53.3
Pignut hickory	49.3	73.7	78.4	100.0	79.2
Red maple	48.7	79.9	97.3	100.0	85.0
American basswood	48.1	40.2	45.9	9.5	32.2
Mockernut hickory	47.1	77.9	97.3	98.6	80.0
Blackjack oak	44.8	72.6	77.5	100.0	77.5
Post oak	44.7	75.9	97.3	100.0	84.2
Eastern hemlock	44.7	53.8	72.9	NA	35.8
Silver maple	44.7	48.1	92.7	30.0	27.9
Red spruce	44.0	21.2	4.6	NA	NA
Virginia pine	43.1	69.7	97.3	56.3	72.4
Southern red oak	38.1	72.2	94.6	91.7	63.8
Quaking aspen	37.8	1.4	0.0	NA	NA
Chestnut oak	37.8	63.1	96.4	44.0	56.5
Yellow birch	37.0	29.2	NA	33.1	20.5
Tulip poplar	35.9	61.1	81.1	93.1	70.5
Shortleaf pine	35.8	73.8	97.3	100.0	70.8
Winged elm	34.8	72.3	73.9	100.0	55.9
Sweetgum	34.5	68.7	97.3	97.2	68.2
Loblolly pine	34.0	68.3	97.3	91.7	60.8
Striped maple	29.9	47.2	NA	32.2	29.4
Balsam fir	28.6	3.7	0.3	NA	0.0
Black hickory	27.9	45.8	62.2	100.0	77.5
Longleaf pine	13.7	21.3	48.5	93.1	23.5
Slash pine	13.0	22.8	90.8	15.3	25.1
Table mountain pine	6.4	12.7	20.1	NA	0.0
Mountain maple	1.3	0.3	2.2	18.9	9.4
Average (high GHG)	39.8	55.1	73.0	76.3	51.5
Low GHG emissions					
Black oak	75.4	96.9	94.6	100.0	90.8
White oak	73.6	98.1	97.3	100.0	95.8
Black cherry	73.3	97.0	97.3	98.6	95.8
Northern red oak	72.9	90.5	97.3	98.6	85.8
White ash	72.3	92.9	97.3	98.6	68.5
American elm	71.7	84.4	95.5	87.5	38.3
Pignut hickory	67.0	94.0	97.3	100.0	77.1
Sugar maple	65.6	75.8	97.3	66.7	67.1
Red maple	64.4	97.9	97.3	100.0	97.5
Mockernut hickory	64.1	97.1	97.3	100.0	85.0
Post oak	63.9	83.1	33.1	100.0	80.0
Shagbark hickory	62.9	72.9	59.5	73.6	55.2
Southern red oak	59.1	79.5	21.0	98.6	87.5
Loblolly pine	56.3	70.7	27.4	85.8	80.1
Silver maple	55.5	36.3	39.6	18.1	8.4
Blackjack oak	54.1	75.6	25.2	95.8	56.5

Table 3. continued

Species	Eastern U.S.	ALCC	DEWA PACE	SHEN PACE	GRSM PACE
Shortleaf pine	52.6	82.9	26.5	100.0	88.8
American basswood	51.5	35.2	92.8	12.5	15.6
American beech	50.8	78.1	97.3	68.1	87.5
Sweetgum	50.4	75.0	45.0	86.1	74.6
Balsam fir	50.1	1.3	0.0	NA	NA
Black hickory	46.9	53.7	46.2	93.1	35.7
Tulip poplar	45.8	86.6	94.6	91.7	94.2
Quaking aspen	45.1	13.7	35.1	NA	1.9
Virginia pine	43.4	73.0	55.0	94.4	84.7
Winged elm	43.1	75.7	22.5	98.6	60.7
Red spruce	36.3	7.2	23.4	NA	11.9
Chestnut oak	34.2	79.2	97.3	97.2	84.2
Eastern hemlock	32.5	50.4	95.5	48.1	60.4
Slash pine	32.1	25.1	NA	NA	12.1
Longleaf pine	28.1	22.0	0.0	13.3	22.0
Yellow birch	24.9	21.4	79.3	0.0	54.9
Striped maple	18.8	33.0	57.7	29.0	46.8
Table mountain pine	5.2	10.3	0.0	24.5	24.7
Mountain maple	2.5	1.0	2.7	0.0	3.0
Average (low GHG)	49.9	61.9	60.1	73.5	59.8
Average (high and low GHG)	44.9	58.5	66.5	74.9	55.7

NA (not available) values indicate the species was not projected as present in the area of interest.

future forest habitat composition of northern PACEs was generally more similar to the current forest composition of southern PACEs under high GHG emissions projections (Appendix E in supplementary material).

DISCUSSION

Our results show general correspondence between the modeling efforts in that the potential impact of climate change on tree species habitat space in the eastern U.S. is substantial. There was consensus that habitat space will shift rapidly and decrease for many species, but there was less certainty in which species will gain habitat space and the amount gained. These uncertainties are likely explained by differences between the studies, including the modeling approaches, predictor variables, spatial resolution, GCMs, and emissions scenarios, prompting several key questions: why might model correspondence vary by spatial scale and species? What are the implications for the management of these species in protected areas?

We first reiterate that model ''correspondence'' refers to the congruence between model projections of tree species habitat response to climate by 2100. As expected, higher temperatures associated with high GHG emissions likely amplified the differences in modeling approaches (for example, habitat forecasting), resulting in lower model correspondence. The difference in high GHG emissions scenarios considered (A1FI vs. A2) likely influenced correspondence and ultimately contributed to the differences between ANUCLIM and RF model fitting and forecasting. For instance, the generally lower model congruence for species in GRSM PACE is likely attributed (in part) to the influence of southern Appalachian topography and climate on the projections derived from ANUCLIM, which relies on elevation for the spatial interpolation of climate data. This could partly explain the more distinct latitudinal gradient in suitable habitat projections by McKenney and others (2011), whereby suitable habitat decreases in the piedmont region for some species that Iverson and others (2008a, b) project to maintain suitable habitat, likely owing to more favorable soil conditions (for example, longleaf and loblolly pine). The data from McKenney and others (2011) likely project larger habitat shifts (for example, mean center) because their models were based solely on climate variables, rather than a combination of climatic and non-climatic variables (for example, soil, disturbance) included by Iverson and others (2008a). We do not

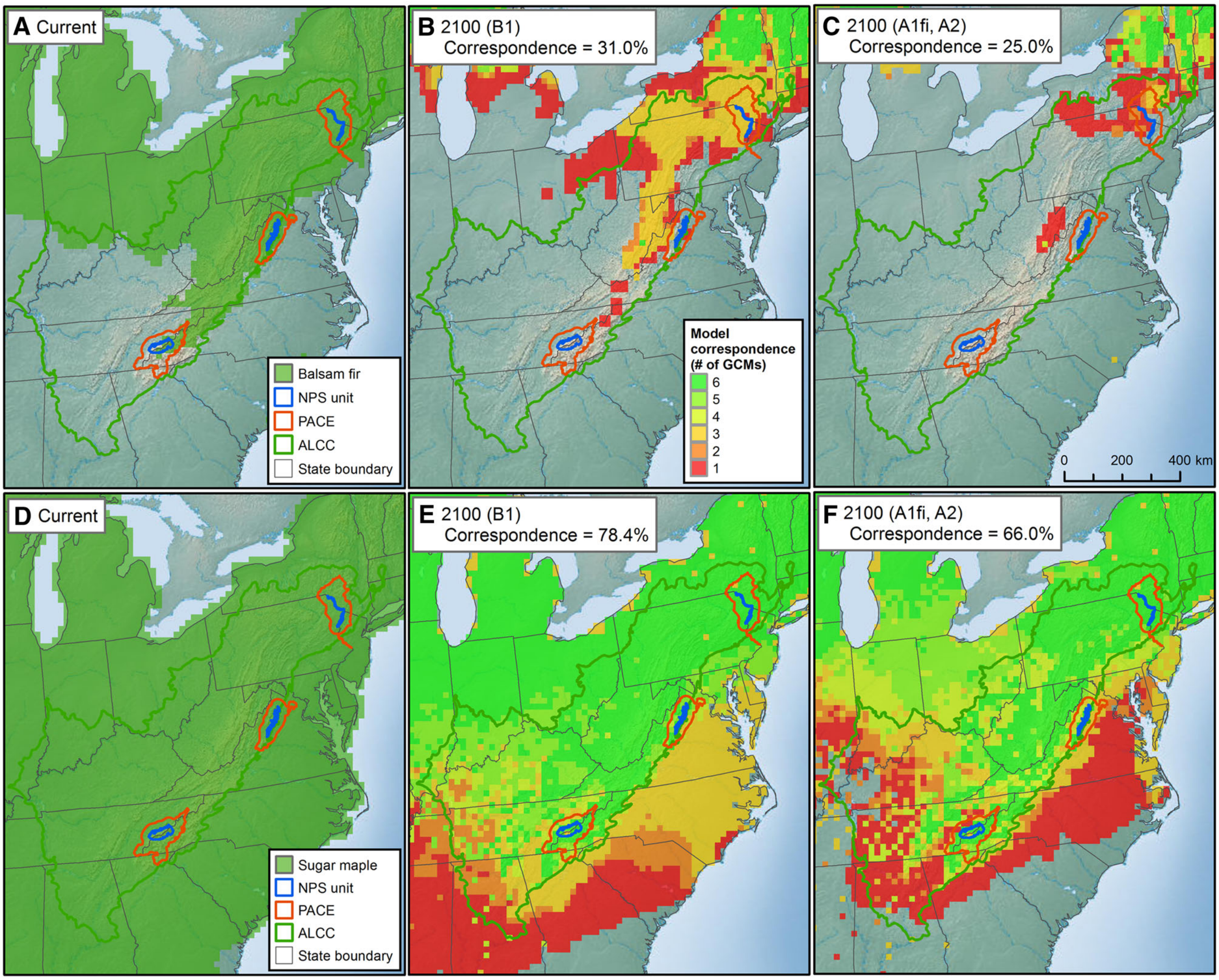

Figure 2. Balsam fir (**A**–**C**) and sugar maple (**D**–**F**) distribution maps at present (**A**, **C**; represented by the union of the current range from Iverson and others 2008a and McKenney and others 2011) and projected for 2100 under low (**B**, **E**) and high (**C**, **F**) GHG emissions scenarios. Projected distributions are mapped for all six GCMs evaluated by Iverson and others (2008a) and McKenney and others (2011), including the average correspondence between GCM projections across the ALCC. A1FI, A2, B1 = greenhouse gas emissions scenarios (Table 1), NPS = National Park Service, PACE = Protected Area Centered Ecosystem, ALCC = Appalachian Landscape Conservation Cooperative, GCM = general circulation model. Base map from Esri ArcGIS online (Color figure online).

imply that complex models are inherently more robust, but rather the McKenney and others (2011) models were purely driven by climate.

Model correspondence across spatial scales was clearly more complex than we anticipated, likely owing to the relative importance of bioclimatic, topo-edaphic, and landscape disturbance variables in the two modeling approaches. We expected correspondence to decrease at finer spatial scales as climatic factors gave way to topo-edaphic factors that more strongly regulate species distributions at finer spatial scales (for example, Pearson and Dawson 2003), yet we found that correspondence often increased. It was reasonable to expect that model correspondence would increase for tree species occupying larger areas of a focal area because there is more opportunity for areal overlap. Although this was generally true, the hypothesized relationship between species occurrence and model correspondence did not necessarily hold for all species at finer spatial scales (for example, PACEs), where topography, disturbance, and soils were expected to drive lower model correspondence. Species meeting this expectation included balsam fir (average correspondence = 0–4% under high and low GHG emissions), for which Iverson and

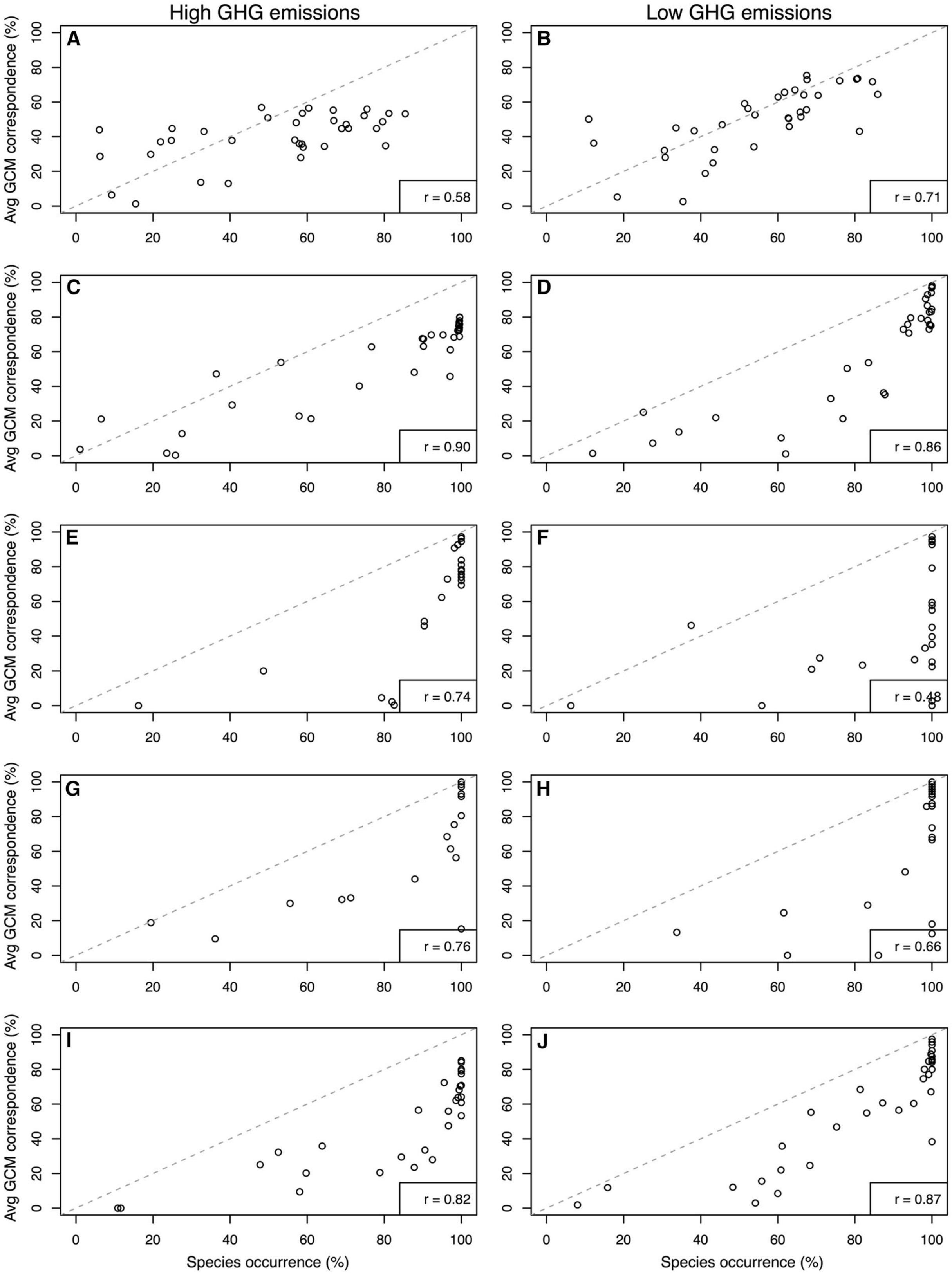

Figure 3. Scatterplots of average GCM correspondence versus species occurence in the eastern U.S. (**A**, **B**), ALCC (**C**, **D**), DEWA PACE (**E**, **F**), SHEN PACE (**G**, **H**), and GRSM PACE (**I**, **J**) for 35 tree species, except for panels **F** and **J** (*n* = 34); **E** and **I** (*n* = 33); **H** (*n* = 31); and **G** (*n* = 30). GHG = greenhouse gas emissions, GCM = general circulation model.

others (2008a) ranked average elevation as a top predictor variable. However, the decrease in balsam fir habitat congruence at the PACE scale could have been driven by the decrease in size of the focal area, resulting in fewer opportunities for spatial overlap that would be possible across the species' full range. American basswood exhibited this trend, whereby its models were in higher correspondence, it had greater occurrence, and elevation was among the top predictors of its habitat. Although the anticipated inverse relationship between model correspondence and the importance of elevation was more variable than expected, precipitation and soil variables were frequently top predictors of tree species habitat (at the eastern U.S. scale) for species that were in higher correspondence (≥75th percentile of correspondence) at the PACE scale, whereas temperature and soil variables were important predictors for most tree species that were in lower correspondence in PACEs. This observation might be attributable to the inclusion of soil predictor variables by Iverson and others (2008a), resulting in greater opportunity for species to be fixed to more favorable habitat conditions in a specific area, whereas the climate-driven approach by McKenney and others (2011) allows for greater range shifts. Although precipitation, temperature, and soil variables are key drivers of tree species distributions, forest managers who are building conservation strategies upon SDM habitat projections might duly note the lower model congruence in PACEs for temperature-driven species and that developing management strategies for these species could prove particularly challenging.

A number of factors contributing to the extirpation (or persistence) of species in particular areas that we did not account for in this analysis suggest that these results may underestimate the potential impacts of climate change on tree species decline and associated ecosystem vulnerability. Drought stress is not explicitly considered in the models we analyze and is fundamental to vapor pressure deficit (VPD)-induced effects including forest productivity declines and mortality (Bréda and others 2006; Allen and others 2010; Williams and others 2013). Increasing VPD and drought stress under future warming could thus alter forest composition and structure (Williams and others 2013). For instance, white ash, a widely distributed species in the eastern U.S., is potentially more vulnerable to climate change than reflected by these models because precipitation and available water capacity are among the most influential bioclimatic factors influencing its distributions, even though the projections for white ash correspond reasonably well in the ALCC. Previous research suggests that white ash is among the tree species projected to respond most negatively to disturbance threats, particularly from the emerald ash borer, thus compounding the detrimental impacts of climate-induced habitat shifts (Matthews and others 2011). Disturbance (for example, pests, habitat fragmentation) might suppress tree species migration rates and promote general tree species decline, yet tree species entering regions occupied by vulnerable species (for example, balsam fir) could flourish more than expected. However, the possibility that tree species projected to face intense pressure by climate change could adapt (somewhat) in the near term offers some hope. For instance, northern, cold-adapted species (balsam fir, quaking aspen, and red spruce) were projected to lose more than 60% of their habitat space in the ALCC under ensemble average (high and low) GHG emissions projections. Although these tree species could be vulnerable to climate change in the long-term, their adaptive response to environmental stress (for example, epigenetics; Nicotra and others 2010) in the coming decades is unaccounted for in our results. If strong adaptive capacity promotes their near-term persistence, then regions of stable habitat space (that is, overlapping current and future suitable habitat) identified in these results could serve as areas for targeted conservation.

Although the large projected magnitude of forest redistribution under climate change during this century will likely challenge forest management in the eastern U.S. protected areas and potentially drive species from reserves (for example, Burns and others 2003; Araújo and others 2004; Lemieux and Scott 2005), these observations suggest that there is an abundance of high-priority conservation space both within and outside of PACEs but still within the ALCC. Tree species representation could be maintained within ALCC protected areas, so long as range shifts occur within the protected area boundary, or outside of protected areas if (1) the dispersal ability of the species and (2) the distance, connectivity, and intermediate land use promote migration to other conservation areas (for example, Midgley and others 2002; Pearson and Dawson 2003; Gaston and others 2008; Jantz and others 2014). For instance, red spruce was projected to occupy new habitat space both in the DEWA PACE and the Adirondack Mountains of north central New York State, but the latter region is likely too great a distance to naturally migrate by 2100. In the latter scenario, in which habitat space shifts outside of ALCC parks or PACEs, the early implementation of conservation efforts would likely result in greater

Table 4. Suitable Habitat Space Change (ΔSHS) for All Tree Species by 2100 for Three Focal Areas, Averaged for Three General Circulation Models (GCM) and Emissions Scenarios (B1, A2, A1FI), Ranging from Low to High Radiative Forcing

Common name	Focal area	Avg Lo (B1)[a]	Avg Lo (B1)[b]	Avg Hi (A1FI)[a]	Avg Hi (A2)[b]
Balsam fir	Eastern U.S.	0.62	0.29	0.56	0.07
Striped maple	Eastern U.S.	0.76	0.66	0.64	0.31
Red maple	Eastern U.S.	1.01	0.79	1.04	0.53
Silver maple	Eastern U.S.	1.45	0.72	2.04	0.46
Sugar maple	Eastern U.S.	0.9	0.73	0.8	0.47
Mountain maple	Eastern U.S.	0.23	0.62	0.08	0.27
Yellow birch	Eastern U.S.	0.71	0.68	0.58	0.34
Pignut hickory	Eastern U.S.	1.18	0.8	1.36	0.56
Shagbark hickory	Eastern U.S.	1.32	0.78	1.57	0.55
Black hickory	Eastern U.S.	3.74	0.82	5.27	0.6
Mockernut hickory	Eastern U.S.	1.18	0.83	1.37	0.6
American beech	Eastern U.S.	0.94	0.75	0.93	0.5
White ash	Eastern U.S.	1.23	0.77	1.39	0.53
Sweetgum	Eastern U.S.	1.27	0.83	1.48	0.57
Tulip poplar	Eastern U.S.	1.13	0.7	1.34	0.43
Red spruce	Eastern U.S.	0.86	0.49	0.87	0.18
Shortleaf pine	Eastern U.S.	1.45	0.81	1.77	0.58
Slash pine	Eastern U.S.	1.78	0.6	2.63	0.34
Longleaf pine	Eastern U.S.	1	0.68	1	0.42
Table mountain pine	Eastern U.S.	1.25	0.6	1.5	0.29
Loblolly pine	Eastern U.S.	1.35	0.86	1.65	0.58
Virginia pine	Eastern U.S.	1.09	0.8	1.41	0.53
Quaking aspen	Eastern U.S.	0.69	0.65	0.82	0.29
Black cherry	Eastern U.S.	1.03	0.78	1.01	0.51
White oak	Eastern U.S.	1.11	0.77	1.22	0.53
Southern red oak	Eastern U.S.	1.33	0.85	1.62	0.6
Blackjack oak	Eastern U.S.	2.66	0.85	3.56	0.62
Chestnut oak	Eastern U.S.	1.01	0.73	1.19	0.44
Northern red oak	Eastern U.S.	1.03	0.73	1.02	0.47
Post oak	Eastern U.S.	1.56	0.86	1.87	0.64
Black oak	Eastern U.S.	1.14	0.76	1.23	0.53
American basswood	Eastern U.S.	1.04	0.74	1.24	0.49
Eastern hemlock	Eastern U.S.	0.83	0.69	0.79	0.36
Winged elm	Eastern U.S.	2.18	0.84	2.74	0.58
American elm	Eastern U.S.	1.14	0.77	1.27	0.53
Balsam fir	ALCC	0.05	0.29	0.05	0.03
Striped maple	ALCC	0.71	0.73	0.6	0.34
Red maple	ALCC	1	0.99	1.01	0.8
Silver maple	ALCC	1.52	0.88	3.15	0.64
Sugar maple	ALCC	0.78	0.91	0.63	0.66
Mountain maple	ALCC	0.95	0.65	0.92	0.27
Yellow birch	ALCC	0.64	0.76	0.52	0.39
Pignut hickory	ALCC	1.05	0.95	1.05	0.74
Shagbark hickory	ALCC	1.35	0.88	1.58	0.67
Black hickory	ALCC	11.72	1.09	14.33	1
Mockernut hickory	ALCC	1.06	0.98	1.06	0.78
American beech	ALCC	0.86	0.95	0.84	0.73
White ash	ALCC	1.06	0.96	1.1	0.76
Sweetgum	ALCC	1.79	1.06	2.11	0.85
Tulip poplar	ALCC	1.07	0.88	1.07	0.61
Red spruce	ALCC	0.42	0.41	0.56	0.09
Shortleaf pine	ALCC	2	1.14	2.27	0.91
Slash pine	ALCC	7.61	1.38	29.11	2.05

Table 4. continued

Common name	Focal area	Avg Lo (B1)[a]	Avg Lo (B1)[b]	Avg Hi (A1FI)[a]	Avg Hi (A2)[b]
Longleaf pine	ALCC	1	1.61	1	1.76
Table mountain pine	ALCC	1.25	0.62	1.48	0.25
Loblolly pine	ALCC	2.27	1.17	2.91	0.99
Virginia pine	ALCC	1.13	1.04	1.24	0.8
Quaking aspen	ALCC	0.27	0.53	0.43	0.25
Black cherry	ALCC	1	0.98	1	0.78
White oak	ALCC	1.01	0.99	1.01	0.8
Southern red oak	ALCC	1.99	1.18	2.39	1.01
Blackjack oak	ALCC	4.99	1.03	6.06	0.82
Chestnut oak	ALCC	0.98	0.88	1	0.6
Northern red oak	ALCC	0.96	0.92	0.95	0.68
Post oak	ALCC	1.86	1.12	2.11	0.91
Black oak	ALCC	1.07	0.98	1.07	0.77
American basswood	ALCC	0.71	0.88	0.89	0.66
Eastern hemlock	ALCC	0.86	0.75	0.88	0.39
Winged elm	ALCC	2.47	1	2.98	0.81
American elm	ALCC	1.25	0.99	1.39	0.81
Balsam fir	PACE	0	0.44	0	0.13
Striped maple	PACE	0.7	0.8	0.61	0.5
Red maple	PACE	1	1	1	0.95
Silver maple	PACE	3.5	0.93	9.61	0.81
Sugar maple	PACE	0.85	0.95	0.78	0.81
Mountain maple	PACE	0.67	0.73	0.44	0.41
Yellow birch	PACE	0.9	0.85	0.86	0.56
Pignut hickory	PACE	1.1	0.92	1.1	0.86
Shagbark hickory	PACE	2.8	0.92	3.85	0.86
Black hickory	PACE	13	1.5	21.67	1.69
Mockernut hickory	PACE	1.13	0.95	1.13	0.9
American beech	PACE	0.89	0.99	0.87	0.89
White ash	PACE	1.14	0.91	1.28	0.87
Sweetgum	PACE	3.1	1.18	3.93	1.12
Tulip poplar	PACE	1.21	0.99	1.22	0.8
Red spruce	PACE	0.67	0.44	0.75	0.18
Shortleaf pine	PACE	1.48	1.31	1.91	1.27
Slash pine	PACE	1.11	1.61	6.33	2.6
Longleaf pine	PACE	1	2.84	1	3.83
Table mountain pine	PACE	1.25	0.7	1.63	0.4
Loblolly pine	PACE	1.68	1.41	2.27	1.52
Virginia pine	PACE	1.21	1.2	1.41	1.1
Quaking aspen	PACE	0.19	0.55	0.06	0.35
Black cherry	PACE	1	1	1.01	0.93
White oak	PACE	1.04	0.99	1.04	0.94
Southern red oak	PACE	1.89	1.37	2.53	1.52
Blackjack oak	PACE	7.13	1.06	11	1.02
Chestnut oak	PACE	1.04	0.95	1.04	0.77
Northern red oak	PACE	1	0.95	1	0.83
Post oak	PACE	2.09	1.28	2.7	1.24
Black oak	PACE	1.2	0.97	1.21	0.9
American basswood	PACE	1	0.9	1.18	0.81
Eastern hemlock	PACE	0.98	0.84	0.98	0.55
Winged elm	PACE	3.87	1.02	5.82	0.97
American elm	PACE	1.41	1	1.79	0.96

Protected Area Centered Ecosystems (PACE) values represent all three focal areas in the Appalachian Landscape Conservation Cooperative (ALCC).

[a] *Calculated using data from Iverson and others (2008a).*

[b] *Calculated using data from McKenney and others (2011).*

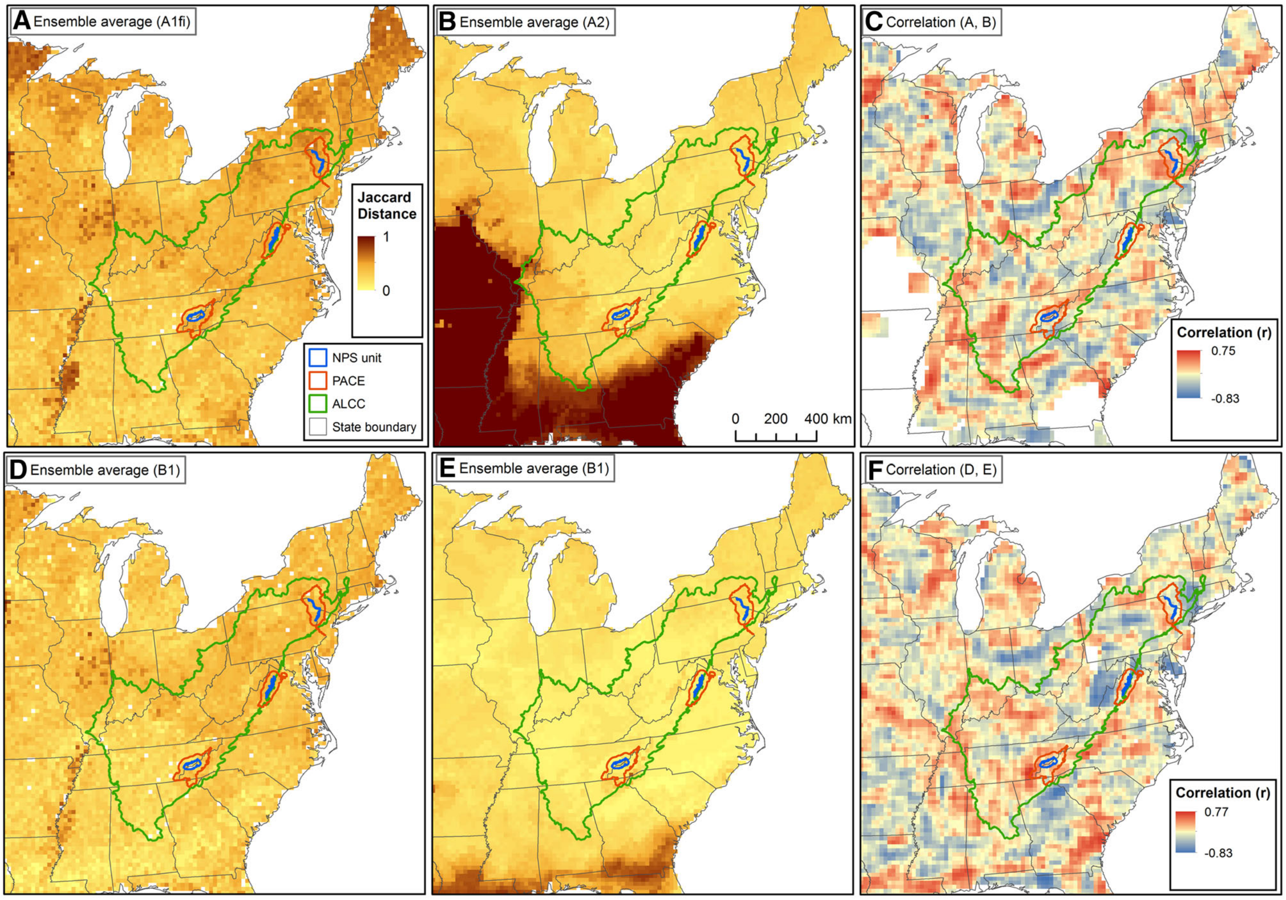

Figure 4. Jaccard distance values (per-grid cell) for 35 tree species across protected areas in the eastern U.S. from suitable habitat space projections by Iverson and others (2008a) (**A**, **D**) and McKenney and others (2011) (**B**, **E**) under respective ensemble high (**A**, **B**) and low (**D**, **E**) GHG emissions projections, and their spatial correlation (**C**, **F**). For Jaccard distance maps, values approaching 1 indicate increasing dissimilarity in forest composition (that is, the species present). A1FI, A2, B1 = greenhouse gas emissions scenarios (Table 1), NPS = National Park Service, PACE = Protected Area Centered Ecosystem, ALCC = Appalachian Landscape Conservation Cooperative (Color figure online).

opportunities for successful conservation. However, tree species will not necessarily migrate to potential habitat space, especially to isolated patches that are distant from the present range. Although red spruce might persist along the Appalachian corridor where current and future habitat space is close and/or overlaps, its establishment in distant (>50 km) habitat space in northwestern Pennsylvania and north central New York State is unlikely without assistance, owing to the rarity of long-distance dispersal events and limited evidence for expansion of certain tree seedling ranges northward under climate change (Pearson 2006; Woodall and others 2009; Zhu and others 2012; Iverson and McKenzie 2013). Thus, management efforts might promote the long-term survival of tree species through population translocation, ex situ conservation (that is, in areas of suitable habitat space), or by increasing the effective size of protected areas through increased connectivity (for example, Diamond 1975; Araújo and others 2004; Iverson and McKenzie 2013; Jantz and others 2014).

Given the rapid shifts in tree species habitats expected during the coming century, enhancing connectivity, conserving migration ‘‘corridors’’, or augmenting protected areas to include ecosystems encompassing park units (that is, PACEs) could reduce species vulnerability to climate change over longer time scales by connecting current and future suitable habitat conditions (Goetz and others 2009; Jantz and others 2014) or by decreasing isolation and edge effects, particularly for species projected to lose habitat space in park units or those within migration distance of a PACE. Although the amount of private land in PACEs with high rates of land-use change may impede conservation (Hansen and others 2011), PACEs in the ALCC are at the epicenter of tree species redistribution in the eastern U.S. and will likely promote the persistence and propagation of tree species. Preliminary results from our continuing research indicate that future habitat conditions in the northern ALCC (for example, DEWA PACE) were analogous to current habitats in GRSM PACE. Increased protected area connectivity across the ALCC could thus be an effective conservation strategy to promote the migration of tree species to areas in northern PACEs that could become important habitat. Reducing tree species vulnerability to climate change will require such forward-looking management strategies to conserve ecosystem services associated with healthy forests. Furthermore, future conservation could benefit from higher-resolution inventories and SDMs to delineate migration corridors between these PACEs to understand and promote tree species persistence.

Tree species that could be targeted for conservation with reasonable confidence include those with fairly strong correspondence between redistribution projections (for example, sugar maple). However, the species we found to have high GCM correspondence are often more common species in the ALCC (that is, greater occurrence) and are thus potentially more resilient to projected climate change during the next century. The potential redistribution of species that could face extirpation from ALCC protected areas in the near term—generally those with smaller ranges or endemic to higher elevations (for example, balsam fir)—were often weakly corresponding between the modeling efforts. Thus, further research with local refinements is needed for active conservation and management of such species, whereas higher-resolution SDM is ultimately needed to guide spatially explicit, within-park management decisions (for example, GRSM is ~2,000 km^2, only five times the area of a 400 km^2 grid cell in this study). In terms of maintaining tree species, we suggest that high-priority conservation regions in the ALCC, or focal areas for higher-resolution SDM, could include (1) regions from which habitat space could originate (an area of active research, for example, Koven 2013); (2) potential areas of new suitable habitat (especially for species projected to have contracted ranges) that are in high correspondence between modeling efforts; (3) areas where current and future suitable habitat space could overlap (that is, range stability), particularly in protected areas (for example, Hannah and others 2007); and in areas of future suitable habitat space within reasonable migration distance of current habitat space (~30 km, for example, Schwartz 1993; Davis and Shaw 2001).

We emphasize the importance of a cross-jurisdictional approach to eastern U.S. forest management that incorporates forward-looking management of novel habitat conditions, in addition to the conservation of threatened species currently within protected areas. Such an approach could reduce costs associated with expanding current protected areas to accommodate tree species persistence, while increasing conservation efficiency by decreasing the geographic isolation of protected areas (for example, Hannah and others 2007). Future tree species redistribution will occur across administrative boundaries and quite possibly require international collaborations to effectively conserve species and their habitats. Thus, landscape-scale conservation efforts that coordinate sub-landscape-scale forest management (that is, Landscape Conservation Cooperatives, or LCCs) will be integral in reducing the potential impact of climate change on tree species by increasing the effective size of protected areas (for example, through increased connectivity) or, if sufficient evidence is assimilated, assisting in the migration of key species.

CONCLUSION

The results from our analysis of tree species modeling efforts under climate change in the eastern U.S. were in agreement that a high GHG emissions future will cause considerable changes in tree species suitable habitat space (declines) and distribution (northward migration) across the eastern U.S. in the coming century. The models considered projected shifts in canopy-dominant species that will likely result in the restructuring of ecological systems. Consequent changes in forest composition will impact the vegetation and animal species (including humans) reliant on the ecosystem services provided by the ecological systems with which they interact. Even efforts toward global environmental sustainability and a lower emissions pathway will not prevent more rapid shifts in habitat space (that is, sometimes hundreds of km) than tree species have historically accommodated. The foreseeable range shifts warrant considerable mitigation efforts to protect remnant tree populations under climate change, and additional adaptation efforts to conserve the ecological integrity of eastern forests. Although it is unlikely that all tree species losses can be prevented, efficient conservation strategies can promote their persistence through cross-jurisdictional management, improving connectivity between existing protected areas, and fostering transitions to species better adapted to future conditions.

Based on these results and considerations, we propose two broadly actionable items. First, conservation of key tree species can be accomplished via four management actions: (1) the integration of PACE and Park units through enhanced, collaborative regional forest management directed at the ecosystems surrounding NPS units (for example, Gaston and others 2008; Hansen and others 2011); (2) increasing protected area connectivity and protecting areas in close proximity to current range boundaries to promote species migration; (3) the proactive protection of areas that are projected to contain suitable habitat space for key species (for example, central NY state); (4) assisted migration and establishment of tree species (Pedlar and others 2012). These actions will result in more comprehensive protection of tree species in both their current and future habitats, and promote the conservation of functional ecological systems. A corollary need is to better understand where the range boundaries occur, at a relatively high resolution, so that appropriate management can be identified (Peters and others 2013). Second, we propose higher-resolution modeling to better understand the role of variables related to species distribution change within NPS units (for example, soil type, local topography, and biotic interactions), which would help guide spatially explicit, within-park management decisions. Increased resolution of climate model predictions (for example, TOPS; Nemani and others 2009; Thrasher and others 2013) should facilitate higher-resolution modeling with management implications. Finally, we note that mitigating the effects of climate change on eastern U.S. forests must be collaborative between researchers and managers, and driven by science-based policy formulation and implementation.

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