

Article

# Analysis of Climate Change Impacts on Tree Species of the Eastern US: Results of DISTRIB-II Modeling

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**Abstract:** Forests across the globe are faced with a rapidly changing climate and an enhanced understanding of how these changing conditions may impact these vital resources is needed. Our approach is to use DISTRIB-II, an updated version of the Random Forest DISTRIB model, to model 125 tree species individually from the eastern United States to quantify potential current and future habitat responses under two Representative Concentration Pathways (RCP 8.5 -high emissions which is our current trajectory and RCP 4.5 -lower emissions by implementing energy conservation) and three climate models. Climate change could have large impacts on suitable habitat for tree species in the eastern United States, especially under a high emissions trajectory. On average, of the 125 species, approximately 88 species would gain and 26 species would lose at least 10% of their suitable habitat. The projected change in the center of gravity for each species distribution (i.e., mean center) between current and future habitat moves generally northeast, with 81 species habitat centers potentially moving over 100 km under RCP 8.5. Collectively, our results suggest that many species will experience less pressure in tracking their suitable habitats under a path of lower greenhouse gas emissions.

**Keywords:** climate change; tree species suitable habitat; random forest model; DISTRIB-II; eastern United States

## 1. Introduction

The climate is changing, globally becoming warmer almost every year in recent decades. Risks associated with this warming are high, sometimes manifesting into multiple, broad threats to humanity [1] and the economy [2]. The recent Intergovernmental Panel on Climate Change (IPCC) report on the impacts of global warming of 1.5 °C above pre-industrial levels, and in comparison to impacts of 2.0 °C, describes many ‘Reasons for Concern’ related to efforts to strengthen the global response to the threat of climate change, sustainable development, and efforts to eradicate poverty [3]. Even so, with current pledges in the Paris Agreement on Climate Change, ~2.6–3.2 °C of warming is projected by 2100, though the Agreement aims to limit global warming “well below 2 °C” and to “pursue efforts” to limit temperatures above pre-industrial levels to 1.5 °C [4]. The biodiversity implications of these various levels of warming are huge, as outlined in Warren, et al. [5], where climatically determined geographic range losses exceeding 50% were projected for 44%, 16%, and 8% of plants by 2100, corresponding to warming of 3.2, 2.0, and 1.5 °C, respectively. Even though climatically determined range losses do not equate with actual distributions of plants because trees live a long time while harboring great genetic diversity, the potential effects of climate change on the biota

of the planet are staggering. Meanwhile, the co-benefits of limiting the amount of warming towards the 1.5 °C path are immense.

As a consequence of the range of these potential changes, models are needed to provide a suite of possible outcomes, by species, to assist decision makers to minimize biological impacts and to adapt to the coming changes. Adaptation planning has been accelerating, whether by motivation or mandate. For example, the Northern Institute of Applied Climate Science (NIACS), associated with the USDA Forest Service, has facilitated nearly 300 adaptation demonstrations or projects on forest lands over the last 10 years in the north central and northeastern United States via their Adaptation Workbook [6], [www.forestadaptation.org](http://www.forestadaptation.org). Model outputs are critical for understanding vulnerability and evaluating possible adaptation avenues, particularly when considering transitional or facilitated outcomes [7–9].

To arrive at reliable and informative models of how tree species may respond to a rapidly changing climate, a diverse and dynamic field has emerged, where continued refinement affords new insights. Statistical models and mechanistic models form a dichotomy of how one approaches predicting future change and each has their strengths and weaknesses [10,11]. Demography approaches add another useful dimension to modeling potential futures [12,13], as do paleoecologic studies [14,15]. Hybrid approaches, which use a combination of modeling methods, may also provide key insights not otherwise uncovered [16–19]. Nonetheless, primary themes from all modeling studies indicate the value of forests in the overall climate equation and the high potential for eventual forest composition and productivity changes in the future [20,21].

With passing time, the evidence is mounting that changes are indeed occurring in forest composition and productivity. Evidence of migration of tree species along elevational gradients (up or down) has been mounting for some time, along with the ecological explanations for such movements [22–30]. However, latitudinal or longitudinal changes in species range are more difficult to document because of wide distributions, limited sample size, and confounding disturbance factors, such as insect pests and succession following harvest, forest clearing, fire exclusion, human introductions, or other disturbance [21,31–34]. Nonetheless, recent studies conducted with repeated inventory and demography data do provide insights into changes (or not) in range limits. Boisvert-Marsh and others [35,36] found poleward shifts in Quebec, Canada for *Acer saccharum* Marsh., *Acer rubrum* L., *Fagus grandifolia* Ehrh., and *Betula alleghaniensis* Britt. between 1970–1977 and 2003–2014, mostly attributed to warming of early- or late-season climatic variables. However, they also detected southward shifts of *Abies balsamea* (L.) Mill., *Picea glauca* (Moench) Voss, and *Picea mariana* (Mill.) B.S.P., attributed to natural and human disturbances. Sittaro et al. [37], also in working in Quebec, found that the spatial velocity of temperature at range limits exceeded the pace of tree species migration by a factor of two for 14 of 16 species. Woodall and D’Amato [38], in a decadal evaluation of 20 eastern US tree species not extending north of the Canada border, found stability for 85% of the species, regardless of the level of canopy disturbance.

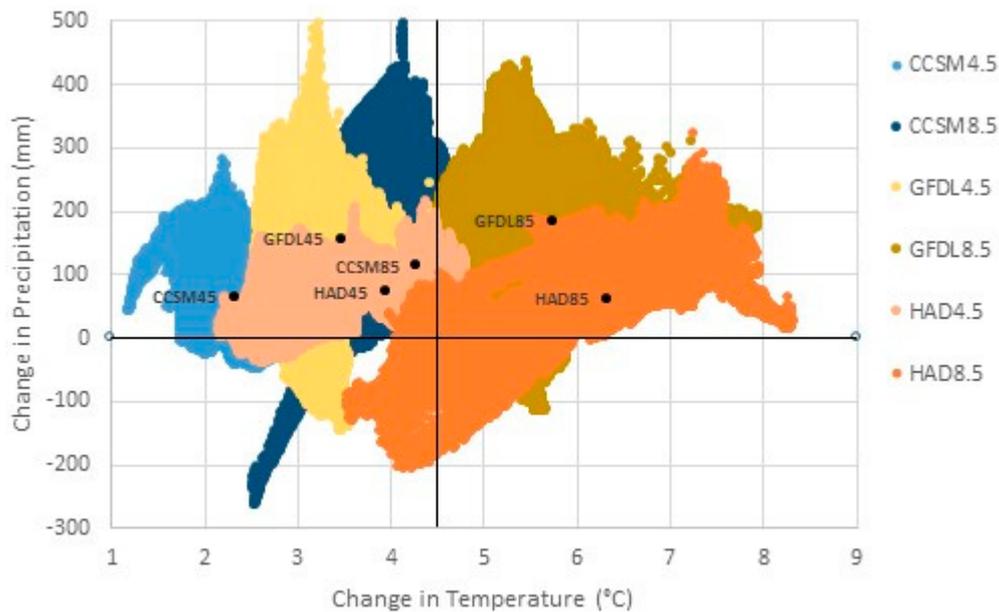
Our modeling approach has been to statistically model potential changes in suitable habitat for a large number to species using Forest Inventory and Analysis (FIA) data and environmental co-variates. This approach has evolved along with concomitant large advances in hardware, data, analytical software, and techniques. Our first effort for 80 common trees used county-level data and the statistical technique Regression Tree Analysis [39,40]. We then moved to a 20 × 20 km grid, 134 tree species, and the Random Forest technique [41–43], our original DISTRIB model which modeled suitable habitat for 134 tree species from the Eastern United States. These models were the basis for several NIACS reports on the vulnerability of forests to climate change in the Mid-Atlantic region [44], the Central Appalachians [45], the Central Hardwoods [46], the Northwoods of Minnesota [47], Michigan [48], and Wisconsin [49], New York and New England [50], and the Chicago Wilderness region [51]. Most recently, we have developed a new set of models based on newer FIA data ([www.fia.fs.fed.us](http://www.fia.fs.fed.us)), higher resolution soils data [52], and a hybrid lattice composed of 10 × 10 km and 20 × 20 km grids, derived from FIA plot density and described in a subsequent paper. The objective of this paper is to summarize the outputs from the DISTRIB-II model, for 125 species of trees in the eastern United States.

## 2. Materials and Methods

In our effort reported here, we present summaries from our recent revision of the original DISTRIB model, now called DISTRIB-II. The extent of our analysis encompasses the United States east of the 100th meridian. In DISTRIB-II, we developed a hybrid lattice of a mix of  $20 \times 20$  and  $10 \times 10$  km cells. The mixture of cell sizes allowed us to optimize modeling by increasing resolution for those cells which had support from sufficient FIA plots. Locations, such as large parts of the Corn Belt in the Midwest, had few FIA plots, so we retained the coarser, 20-km structure, while those locations with higher densities of FIA plots were evaluated and modeled via a 10-km structure. DISTRIB-II also used completely updated data sets of 45 environmental variables and FIA plot data; it also used newer techniques to assign model output values.

### 2.1. Data

**Climate data.** We used a range of models and scenarios to capture projections of future temperature and precipitation. Data included current (1981–2010) annual and seasonal mean temperature ( $^{\circ}\text{C}$ ) and annual and seasonal precipitation totals (mm) based on Parameter-elevation Regressions on Independent Slopes Model, [53] (PRISM), and end of the century (2070–2099) projected mean values from three General Circulation Models (GCM) under the 4.5 and 8.5 Representative Concentration Pathways (RCP). Downscaled future projections were obtained from NASA Earth Exchange U.S. Downscaled Climate Projections (NEX-US-DCP30) project (<https://cds.nccs.nasa.gov/nex/>), with metadata found at ([https://cds.nccs.nasa.gov/wp-content/uploads/2014/04/NEX-DCP30\\_Tech\\_Note\\_v0.pdf](https://cds.nccs.nasa.gov/wp-content/uploads/2014/04/NEX-DCP30_Tech_Note_v0.pdf)) [54]. These data are derived from GCM runs under the Coupled Model Inter-comparison Project Phase 5 (CMIP5) in support of the IPCC Fifth Assessment Report (IPCC AR5). The NEX US-DCP30 dataset was downscaled to  $30 \times 30$  arcseconds via Bias-Correction Spatial Disaggregation (BCSD) [55]. Future values were derived by adjusting PRISM data with the change (the deltas) between GCM-simulated data for periods 1981–2010 and 2070–2099, similar to methods described by Monahan, et al. [56]. These delta adjustments provided closer alignment to current conditions now and minimized exposure to pixel-level artifacts between training and projection climate data. For climate summaries reported in Table 1, data were aggregated to 10-km across 41,681 cells across the eastern U.S. Three models were used, each with RCP 4.5 and 8.5 [57]: Community Climate System Model, or CCSM4 (hereafter CCSM45 and CCSM85) [58], Geophysical Fluid Dynamics Laboratory (Donner), or GFDL-CM3 (GFDL45 and GFDL85) [59], and Hadley Global Environment Model—Earth System [60] (or HadGEM2-ES (Had45 and Had85) [61]. These climate models and RCPs capture, for the entire eastern U.S. study area, a wide distribution space in projected change (Figure 1 and detailed in Table 1). Further, the mean change across these combinations (Figure 1), fall along a strong temperature gradient, from an estimated annual temperature increase of  $2.5^{\circ}\text{C}$  with CCSM45 to  $6.5^{\circ}\text{C}$  with Had85, and with an overall mean increase of  $4.5^{\circ}\text{C}$ . The potential change in annual precipitation (though precipitation changes have higher uncertainty as compared to temperature changes) was higher for all scenarios by end of the century, but for many locations, a reduction in future precipitation is forecasted (i.e., points below the horizontal 0 change line), especially for Had85 and GFDL85 (Figure 1). Coupled with higher temperatures, especially these scenarios will likely inflict additional physiological stress on organisms for some future periods (see also [62]). This trend is especially true when examining growing season temperatures, which reach  $28.4^{\circ}\text{C}$ , an increase of  $6.8^{\circ}\text{C}$ , for both GFDL85 and Had85. To make matters worse for plant growth, the Hadley model (Had45 and Had85) showed growing season precipitation decreases by end of the century, even though annual precipitation was slightly higher (Table 1).



**Figure 1.** Distribution of annual temperature and precipitation changes from a baseline period (1981–2010) as modeled by the NASA Earth Exchange U.S. Downscaled Climate Projections (NEX-US-DCP30) data for 2070–2099, for 41,683 10-km cells across the eastern US. Black dots are the mean change in precipitation and temperature for each General Circulation Models (GCM)-Representative Concentration Pathways (RCP) scenario.

**Table 1.** Average climate conditions in the eastern US currently and for three models (CCSM4, GFDL CM3, and HadGEM2-ES) for the 4.5 and 8.5 RCPs. CCSM4: Community Climate System Model; GFDL CM3: Geophysical Fluid Dynamics Laboratory Coupled Model 3; HadGEM2-ES: Hadley Global Environment Model—Earth System; PANN: Mean Annual Precipitation; Pgrow: Precipitation in growing season; TANN: Mean Annual Temperature; Tgrow: Temperature during growing season (May–Sept); TSUMavg: Mean Temperature of Warmest Month; TWINavg: Mean Temperature in Coldest Month; TMin: Absolute Minimum Temperature; TMax: Absolute Maximum Temperature; RCP: Representative Concentration Pathway.

Variable	CCSM4		GFDL CM3		HadGEM2-ES		
	Current	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
PANN (mm)	1048	1113	1162	1203	1233	1121	1110
Pgrow (mm)	509	527	519	573	585	504	457
TANN (°C)	12.7	15.2	17.1	16.3	18.6	16.8	19.2
Tgrow (°C)	21.6	24.0	26.3	26.0	28.4	25.7	28.4
TSUMavg (°C)	24.8	26.6	28.1	28.1	29.7	28.0	29.9
TWINavg (°C)	−0.9	1.2	2.1	1.6	2.0	1.3	3.3
TMin (°C)	−11.3	−8.6	−6.5	−7.2	−5.7	−7.4	−4.0
TMax (°C)	33.8	35.9	39.3	39.1	42.5	38.5	41.9

**Tree Data.** As done in the earlier effort [42], we used U.S. Forest Service Forest Inventory and Analysis (FIA, [www.fia.fs.fed.us](http://www.fia.fs.fed.us)) data to derive individual tree species importance values (IV) for each of 84,204 FIA plots. All plots were included with no filtering. The assumption was if the species already grows there, it can grow there. The relative number of stems and relative basal area for each species were weighted equally to calculate IV for each plot. Thus, some species with large numbers of smaller stems (e.g., *Ulmus*, *Acer*, *Fraxinus* spp.) may be calculated as more important than species with fewer, but larger stems (e.g., some *Quercus*). All 84,204 annualized FIA records sampled during the period 2000–2016 were processed, and aggregated to cells with native resolutions of either 10 × 10 km or 20 × 20 km to represent the mean IV within the grid cell. We strove to increase spatial resolution,

over that of our previous effort, where the FIA data would support it; to that end, a hybrid lattice was generated through an iterative algorithm to determine whether resolution could be increased to  $10 \times 10$  km (four cells within each  $20 \times 20$  km cell), or maintained at  $20 \times 20$  km. To do so, a 10-km was accepted if  $\geq 50\%$  of the four 10-km cells within a 20-km cell contained two or more FIA plots, otherwise the focal 20-km cell was retained. The resulting hybrid lattice for the eastern U.S. had 29,357 cells, 84.7% of which were comprised of  $10 \times 10$  km cells, and accounting for 2.49 million  $\text{km}^2$ , or 58% of the eastern U.S. (Figure 2). The  $20 \times 20$  km cells occupied 1.79 million  $\text{km}^2$ , or 42% of the area, and were mostly confined to highly agricultural areas, predominantly in the western portion of the eastern U.S. (Figure 2). To minimize species that have too few samples to build a respectable model, species were only included if they had at least 60 grid cells with at least two FIA plots per cell. This filter resulted in a total of 125 species in the analysis.

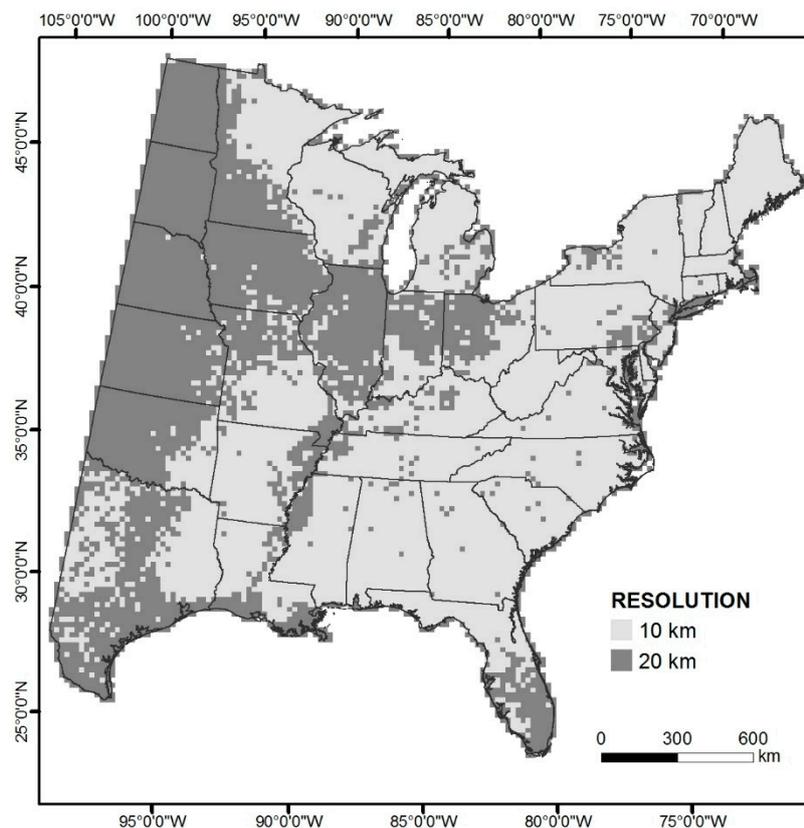


Figure 2. Extent of 20 km vs. 10 km cells used for DISTRIB-II modeling.

**Environmental Data.** A suite of 45 environmental variables was used to predict IV, for 125 species across the entire eastern US. We used seven climate-related variables, seven elevation-related variables, a solar-related variation of day length variable, nine soil taxonomic orders, and 21 variables related to soil properties to derive the Random Forest models [41] predicting current species IV (Table 2). These data were acquired from various sources, with most soils information from gSURRGO [52], elevation data from the shuttle radar topography mission [63], a model of solar radiation via latitude [64], and a model of soil productivity based on soil taxonomy [65]. We then swapped the seven climate-related variables with future (2070–2099) projections of the same variables according to each of the six GCM/RCP combinations (see above), and Random Forest predicted future IVs for each species. It is important to note that we are not using elevation variables as a proxy for climate—we use them to discriminate among species that prefer lower elevation habitats (for example along the coastal plains or swamps) from those that prefer more elevated habitats with rugged terrain. Also, in addition to

improving model fit, the numerous soil variables help restrain the models' response under future climates and distinguish among species that are mostly climate driven vs. those that are less so.

**Table 2.** Environmental data used to predict habitat suitability of eastern U.S. tree species. Data was either aggregated to 10 and 20 km grids or derived from aggregated data.

Category	Variable	Description	Native Resolution
Climate <sup>1</sup>	Annual precipitation	Mean 30-year (1981–2010) monthly precipitation (mm).	800 m
	May–Sept. precipitation	Mean 30-year (1981–2010) monthly precipitation for May–September (mm).	
	Annual mean temperature	Mean 30-year (1981–2010) monthly temperature (°C).	
	May–Sept. mean temperature	Mean 30-year (1981–2010) monthly temperature for May–September (°C).	
	Mean temperature of coldest month	Mean 30-year (1981–2010) monthly temperature of coldest month (°C).	
	Mean temperature of warmest month	Mean 30-year (1981–2010) monthly temperature of warmest month (°C).	
	Aridity Index	A conditional ratio of precipitation and Thornthwaite potential evapotranspiration (see [66])	
Elevation [63]	Minimum	Minimum value	90 m
	Mean	Mean value	
	Maximum	Maximum value	
	Median	Median value	
	Range	Range between minimum and maximum values	
	Standard deviation	Amount of deviance among elevation	
	Coefficient of variation	The CV of elevation	
Solar [64]	Day length coefficient of variation	The CV of 12 monthly day lengths derived from the latitude of grid cells.	10 and 20 km
Soil [52]	Available water capacity (cm)	The quantity of water that the soil is capable of storing for use by plants	30 m
	Available water supply (cm)	The total volume of water that should be available to plants when the soil, inclusive of rock fragments, is at field capacity	
	Bulk density (g/cm <sup>3</sup> )	The oven-dry weight of the soil material <2 mm in size per unit volume of soil at water tension of 1/3 bar	
	Calcium carbonate	The percent of carbonates, by weight, in the fraction of the soil <2 mm in size	
	Cation-exchange capacity	The total amount of extractable cations that can be held by the soil, expressed in terms of milliequivalents per 100 grams of soil at neutrality (pH 7.0) or at some other stated pH	
	Depth to water table (cm)	Depth to a saturated zone in the soil	
	Permeability (cm/h)	Saturated hydraulic conductivity or the ease with which pores in a saturated soil transmit water	
	Erosion K factor	The susceptibility of a soil to sheet and rill erosion by water estimated by the percentage of silt, sand, and organic matter and on soil structure and saturated hydraulic conductivity	

Table 2. Cont.

Category	Variable	Description	Native Resolution
	Erosion T factor (tons/acre/year)	An estimate of the maximum average annual rate of soil erosion by wind and/or water that can occur without affecting crop productivity over a sustained period	
	Percent clay	Mineral soil particles that are <0.002 mm in diameter	
	Percent sand	Mineral soil particles that are 0.05 mm to 2 mm in diameter	
	Percent silt	Mineral soil particles that are 0.002 to 0.05 mm in diameter	
	Organic matter content (% by weight)	Plant and animal residue in soil material <2 mm in diameter at various stages of decomposition	
	pH	A measure of acidity or alkalinity	
	Percent passing sieve No. 10	Soil fraction passing a number 10 sieve (2.00 mm square opening)	
	Percent passing sieve No. 200	Soil fraction passing a number 200 sieve (0.074 mm square opening)	
	Soil productivity [65]	Productivity Index derived from family-level Soil Taxonomy information	
	Soil taxonomic order	The percentage of taxonomic order	
	Soil texture	The percentage of clayey, loamy, sandy, or other texture class defined by USDA standard terms	

<sup>1</sup> PRISM Climate Group. 2014. Oregon State University, <http://prism.oregonstate.edu>.

## 2.2. Modeling

Individual tree species IV were modeled using the randomForest library [67] in R version 3.1.1 [68] (hereafter RF), in which 1001 regression trees were trained with eight randomly selected environmental variables evaluated at each node, and grown to include a minimum of 10 observations. To train the models, only grid cells within the hybrid lattice (10 × 10 or 20 × 20 km) were used that had (1) two or more FIA plots (to ensure representation within each cell), (2) ≥5% forest cover defined by the 2006 NLCD [69] (classes 41, 42, 43, and 90, to exclude very highly agricultural regions), and (3) a mean IV ≤ 1.5 times the inter-quartile range of IVs across all cells (to exclude outliers because they were unlikely to represent the full 100 or 400 km<sup>2</sup>). Each of the 1001 regression trees built by RF provides information about the predicted IV, and the default is to report the mean prediction. However, the random resampling of only eight of 45 variables at each node can result in spurious outcomes due to, for example, omission of an entire class of variables (e.g., climate); while these spurious trees rarely influence overall prediction [70], outliers can influence prediction distributions at a given cell [71]. Therefore, we compared the mean predicted value to the median for each cell; if the median = 0 and among all 1001 predicted values the coefficient of variation ≥2.75, then 0 was used as the predicted IV rather than the mean; which was 0 < IV<sub>mean</sub> < 8 among all species. This “mean-median” combination is a modification to the approach suggested by Roy and Larocque [71] which limits the influence on outlier predictions, minimizing the area of modeled low suitability, due to a few outliers within the 1001 regression trees for each species.

Once the RF model was trained, predictions of IV were made to all 29,357 cells irrespective of cell size within the hybrid lattice, whether or not at least 2 FIA plots were present, or whether percent forest cover was less or more than five percent.

### 2.3. Model Reliability

We created a model reliability (ModRel) score from a series of five metrics obtained from the performance statistics of each of 125 species. These included (1) a pseudo  $R^2$  obtained from the RF model (RF  $R^2$ ); (2) a Fuzzy Kappa (FK) metric which compares outputs of the imputed RF-predicted map to the FIA-derived map [72]; (3) the deviance of the CV (CVdev) among 30 regression trees via bagging [41]; and (4) the stability of the top five variables (Top5) from 30 regression trees, and (5) a true skill statistic (TSS) of the imputed RF. The first four were used previously, described in Iverson et al. [42]. The five variables were normalized to a 0–1 scale and weighted as follows to arrive at a final ModRel score:  $0.33 \times \text{RF } R^2 + 0.33 \times \text{FK} + 0.11 \times \text{CVdev} + 0.11 \times \text{Top5} + 0.11 \times \text{TSS}$  which gives more weighting to RF  $R^2$  and FK, a primary performance metric and a comparison of predicted to observed values, respectively. Then, ModRel scores were assigned to one of four classes: High (ModRel  $\geq 0.7$ ), medium ( $0.7 > \text{ModRel} > 0.54$ ), low ( $0.55 > \text{ModRel} \geq 0.14$ ), and unreliable and excluded from further modeling (ModRel  $< 0.14$ ).

### 2.4. Variable Importance

Each of the 45 predictor variables was scored for all species cumulatively according to a variable importance index, which was the average of three normalized (0–100) scores. First, the variable importance, as calculated within the RF function (percent increase in MSE based original and permuted predictors of the out-of-bag data—see the help for “importance” in randomForest library in R), for each of 125 species was summed. Second, the sum of the reciprocal of ranked predictor importance across all species was calculated; the reciprocal produced higher scores for top ranked variables. Third, the frequency, or count, of the number of times a predictor ranks in the top 10 across all species was tabulated. These metrics allowed comparison among the 45 variables for their value in creating the tree species models. Importantly, these metrics are based on all species across the entire eastern U.S. so that species that have specific requirements will not garner much support with these indicator metrics.

### 2.5. Area-Weighted Importance Values

To incorporate both the area and the relative abundance of each species, we calculated area-weighted importance values for each species. We use area-weighted importance values as a surrogate for the strength of suitable habitat across a species' distribution. The higher the IV score, the higher the tendency for that species to occupy that cell, and the higher the possible basal area of that species within the cell. This measure of suitable habitat is not a probability of occurrence (though likely similar for many species) but rather an indication of the potential of the cell to host the species. Any value above 0 can be considered suitable habitat, though the strength of that habitat varies according to the area-weighted IV score. These values thus provide an estimate of each species' importance based on the IV modeled for each cell (or partial cell), multiplied by the area the cell represents. Because of the variation of grid sizes (100 km<sup>2</sup> or 400 km<sup>2</sup>), due to the hybrid grid structure, and the partial cells especially along coasts, the area-weighted values are truer to their actual and projected future suitable habitat. The ratio of future to present modeled condition represents the potential change of suitable habitat in the future, where values  $>1$  indicate an increase in area-weighted importance and values  $<1$  indicate a decrease.

### 2.6. Changes in Mean Center of Spatial Data

Within ArcGIS 10.3 (ESRI, Redlands, CA, USA), the Mean Center and Directional Distribution functions were used to calculate the current and future 'center of gravity' and directional ellipse within 1 standard deviation, respectively, of species ranges generated by our models. No weighting was applied to the IV, but only cells modeled to have an IV  $> 0$  were considered in the calculation of the mean centers and directional ellipses. The coordinates of the mean center were used to calculate distance

and direction of potential movement of the suitable habitat for each species and were visualized using polar graphs to evaluate potential changes among all species for each scenario of climate change.

### 2.7. Analysis of Dominants, Gainers, and Losers

The area-weighted IV allowed comparison of species prominence and potential change according to the climate scenarios, by spatial domain. These provide valuable supplements to FIA data and state reports ([www.fia.fs.fed.us](http://www.fia.fs.fed.us)) on the current situation for tree species, as the IVs are based on both density (number of stems) and dominance (basal area) simultaneously. We provide this information for each of 37 states and the District of Columbia, and for five regions within the eastern US. Notably, for the six states split by the 100th meridian (our boundary of the eastern U.S.), some forest patches will be missed but the area in those states west of the 100th meridian is dominated by nonforest or western species (not modeled), with the exception of the Black Hills of South Dakota. We ranked each species according to the modeled current IV and selected the top three for each spatial unit and then calculated the potential changes in area-weighted IV, as ratios of future to current IVs, among the various scenarios of climate change.

### 2.8. Species-Level Maps

Maps representing species (abundance and suitable habitat under various scenarios) were generated for each species. Specifically, the maps show outputs of the (1) FIA estimate of current abundance, (2) modeled current distribution, and the future distributions according to the (3) CCSM45, (4) CCSM85, (5) GFDL45, (6) GFDL85, (7) Had45, (8) Had85, (9) mean of all three RCP4.5, and (10) mean of all three RCP8.5 scenarios.

### 2.9. Comparison to Earlier DISTRIB Models

We have been modeling tree species suitable habitat within the eastern U.S. since 1998 [17,39,40,42,43], and there have been changes in many dimensions throughout this period. First, we modeled 80 species at the county level of resolution, then 134 species at  $20 \times 20$  km resolution, and most recently 125 species at a hybrid of  $10 \times 10$  and  $20 \times 20$  km resolution, depending on the density of FIA plots (~forest cover). Throughout the period, there has also been a remarkable improvement in environmental data, especially climate and soils data. And, the modeling improvement from regression tree analysis to random forests [41] was particularly dramatic in enhancing model performance. As expected when using multiple models, updated data sets, or variations in modelling technique, model outcomes will differ between iterations; this is true in this case too.

### 2.10. Scope and Limitations

The models depicted here represent changes in potentially suitable habitat according to scenarios of climate change; they do not depict projections of actual future distributions by 2100. Earlier work has shown that natural migration proceeds at a much slower pace than change in habitat, especially for long-lived trees [17,73–75]. Therefore, our projections of an increase in the range are likely to overestimate the actual distributions by century's end, unless humans get seriously involved in moving species.

Though Random Forest has been shown to be a robust modeling tool, highly resistant to overfitting, we sometimes are making predictions into novel parameter space through extrapolation; nonetheless, the resistance to overfitting of Random Forest predictions gives us confidence that the extrapolations are suitably constrained and are not exaggerated projections [41]. Obviously, not all 125 species models are created equal, and we calculate several metrics to assess model reliability for each species [42].

When we model potential changes in suitable habitat, one would normally expect the greatest impacts to be experienced by young plants at the point of regeneration, when seedlings or saplings are more susceptible to the increased extreme weather events and other ramifications of the changing

climate. However, mature forests are certainly also susceptible, either directly via droughts, especially ‘hot’ droughts [76], or indirectly via pests and pathogens [77]. Because the models are based on FIA inventories of trees >2.5 cm dbh, the regeneration component is not well represented in the model formulations. We are modeling the potential niche space that may be available to species under future climates, which may not be the realized niche because disturbances and extreme events will be operating within the suitable habitats. Though the FIA data, in effect, integrates past disturbances by documenting those species that have survived past events, we cannot anticipate future disturbances (like an exotic pest invasion) that will influence actual future distribution and abundance. Further, we cannot assume that all species are in equilibrium with their current climate or other environmental variables.

### 3. Results and Discussion

#### 3.1. Model Reliability and Variable Importance

Of the 125 species in this assessment, we scored 29 species with high model reliability, 47 with medium, and 49 with lower model reliability. These model reliability classes are presented for each species in Table A1. Admittedly, the cut off values presented in the methods section are arbitrary and adjusting the cut offs would change the proportion of each model reliability class. We chose to stay conservative in assigning the cut offs, leading to a loading of species at the lower end of reliability.

When we scored each of the 45 predictor variables according to a variable importance index, we found the climate variables dominated in importance. In fact, seven of the top nine variables were the climate variables. Of course, several of these variables are correlated with each other across the entire eastern U.S. but will be important locally for particular species. The first and second ranked variables were summer (30-year mean of the warmest month) and winter (30-year mean of the coldest month) temperatures; these indicate some species are limited by cold, some are linked to warm temperatures, and some may be driven by both together. Because these metrics are based on all species across the entire eastern U.S., the wide ranging, generalist species will tend to be correlated with wide ranging temperature or precipitation patterns as well. The day length coefficient of variation among months (based on latitude) was the most influential non-climate variable, followed by soil variables pH, texture (soil fraction passing a sieve with a 2 mm square opening), soil productivity (based on soil taxonomic family), and permeability (saturated hydraulic conductivity). The lower ranked variables, though not rated high for all species together, will rank high for individual species in particular habitats, etc. Though space prevents discussion of individual species and their variables of importance, these will be presented in upcoming updates to our Climate Change Tree Atlas ([www.fs.fed.us/nrs/atlas](http://www.fs.fed.us/nrs/atlas)).

#### 3.2. Potential Changes in Species Area-weighted Importance Values

For the 125 species with acceptable models, Table 3 provides an indication of the quantity of species that may lose (Future: Current ratios < 0.9) or gain (ratios > 1.1) suitable habitat by 2100, as well as those projected to remain somewhat stable (0.9 < ratios < 1.1). Averaged across all scenarios, 88 species showed at least a 10% increase in area-weighted IV, and 26 species showed at least a 10% decrease, with 12 species having little or no change (Table 3). For those 88 species inclined to have increasing habitat, the RCP8.5 scenario showed more species at least doubling habitat (55 species) than under the RCP4.5 scenario (42 species) of lower emissions. Notably, there was not much difference between RCPs for those species losing habitat (Table 3). Species included among those projected to lose substantial habitat are: *Acer nigrum* Michx. f. (black maple), *A. spicatum* Lam. (mountain maple), *Picea mariana* (black spruce), *Populus balsamifera* L. (balsam poplar), *Prunus pensylvanica* L.f. (pin cherry), and *Sorbus americana* Marshall (American mountain-ash) (Table A1). Among those species showing substantial increases in suitable habitat are: *Carpinus caroliniana* Walter (American hornbeam), *Celtis laevigata* Willdenow (sugarberry), *Magnolia grandiflora* L. (southern magnolia), *Ostrya virginiana* (Mill.) K.Koch (eastern hophornbeam), *Pinus echinata* Mill. (shortleaf pine), *P. palustris*

Mill. (longleaf pine), *Quercus falcata* Michx. (southern red oak), *Quercus marilandica* Muenchh. (blackjack oak), *Quercus michauxii* Nutt. (swamp chestnut oak), *Q. nigra* (water oak), *Q. phellos* (willow oak), *Quercus phellos* L. (post oak), *Quercus phellos* L. (live oak), *Taxodium distichum* (L.) Rich. (bald cypress), and *Ulmus alata* Michx. (winged elm) (Table A1).

**Table 3.** Potential species changes in area-weighted importance value for habitat suitability for 125 species in the eastern United States. Allowing for a 10% buffer around the future:current ratio of 1.0 (i.e., no change), values below 0.9 indicates a loss, while values above 1.1 indicate a gain in suitable habitat. Scenarios refer to model (CCSM, GFDL, Had, and mean of all three GCM models) and emission level (RCP 4.5 and 8.5).

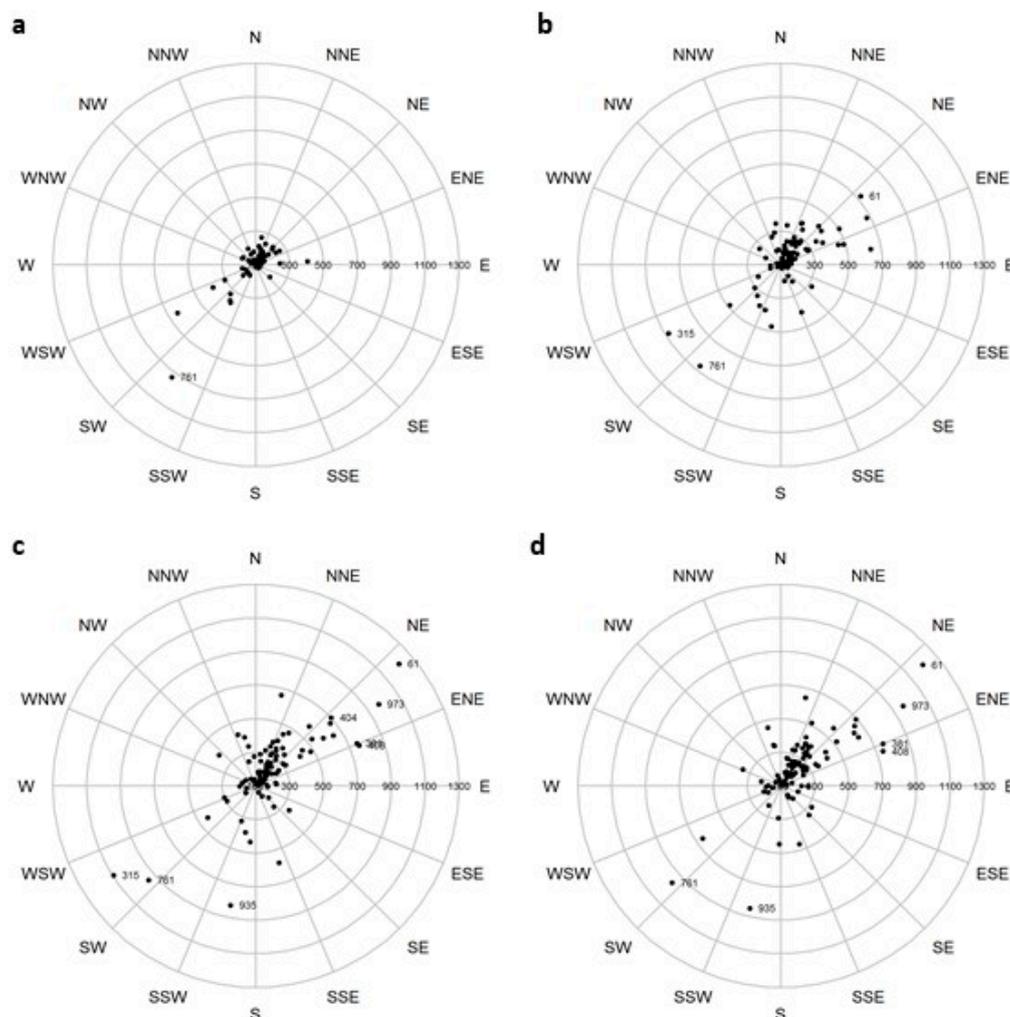
Scenario	Future: Current Ratios of Importance Values					Total
	<0.5	0.5–0.9	0.9–1.1	1.1–2	>2	
CCSM45	6	18	14	64	23	125
CCSM85	7	16	13	40	49	125
GFDL45	8	15	13	39	50	125
GFDL85	6	18	10	31	60	125
HAD45	7	20	12	38	48	125
HAD85	8	24	8	35	50	125
GCM45	8	17	11	47	42	125
GCM85	7	19	9	35	55	125

The data do show that for many of the species gaining in excess of 10% in habitat, they are often from less reliably modeled species than those species losing habitat. For example, only 12 of 88 species (14%) which show at least 10% increase in habitat had highly reliable models, but 12 of 26 species (46%) showing a decrease of at least 10% had highly reliable models (Table A1). For those more common species (arbitrarily selected as those with the sum of IV > 15,000), those ratios are 11 of 34 (32%) for gainers compared to 8 of 8 (100%) for the losers. The large gainers fall into three categories: First, the species is currently common in a region that is now quite warm and fairly dry, that being the southwestern portion of the eastern U.S. (e.g., Texas, Oklahoma, southern Missouri). These species, like *Quercus stellata* (post oak), *Quercus marilandica* Muenchh. (blackjack oak), *Carya texana* Buckley (1861) (black hickory), ashe juniper (*Juniperus ashei* J. Buchholz) and *Juniperus virginiana* L. (eastern red cedar), are primarily temperature driven, and expand greatly in suitable habitat when provided much warmer temperatures as projected under climate change. Second, the species is currently quite rare or sparse according to current FIA plot data, and the models project the species to ‘fill in’ some additional territory with suitable habitat. Species in this category include *Diospyros virginiana* L. (common persimmon), *Ilex opaca* Aiton (American holly), and *Ostrya virginiana* (Mill.) K.Koch (eastern hophornbeam). Third, the species is an important southern species now but is expected to substantially expand its suitable habitat northward by end of the century. These species include *Quercus falcata* (southern red oak), *Quercus nigra* L. (water oak), *Pinus echinata* (shortleaf pine), and *P. palustris* (longleaf pine) (Table A1).

### 3.3. Changes in Mean Center of Spatial Data

The potential changes in mean centers of suitable habitat under various scenarios of climate change indicate that roughly 3–4 times as many species show habitat movement in a northerly direction as compared to a southerly direction (Table 4, Figure 3). As many as 81 species (RCP8.5 mean) could have mean center movement at least 100 km northward. The data also clearly show that those northward-moving species will likely have their mean habitat centers move greater distances under the hotter (RCP8.5) scenarios as compared to the RCP4.5 scenarios. Some of the species modeled to move habitats long distances northward include *Carya texana* (black hickory), *Quercus virginiana* (live oak), and *Ulmus crassifolia* (winged elm) (Figure 3). The scenario with the least change in temperature, CCSM45, also shows less northward movement of mean centers, but this scenario still has 54 species

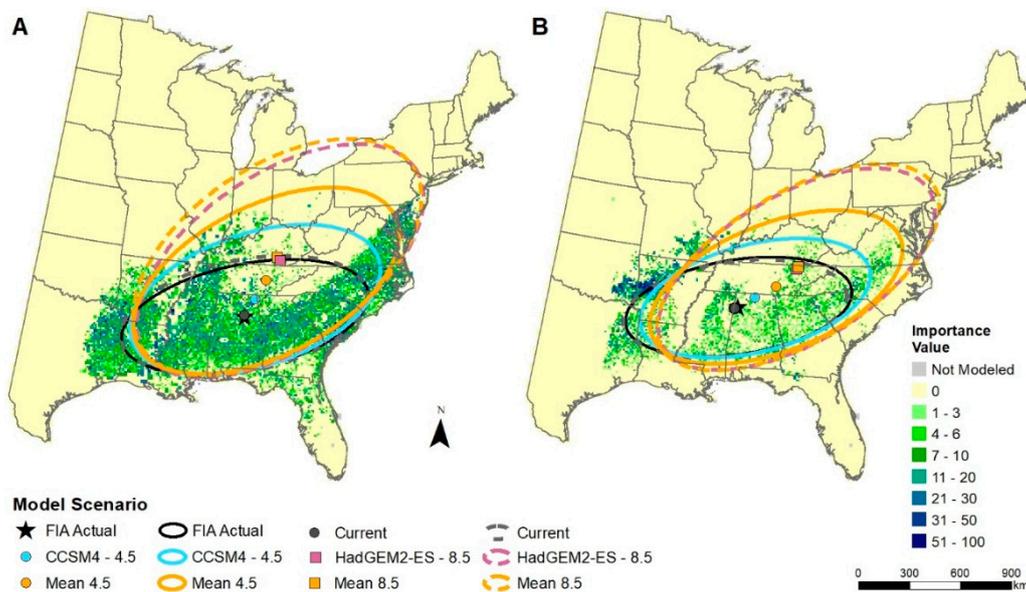
moving habitats at least 100 km by the end of the century. Some of the species moving habitats southward include *Acer pensylvanicum* L. (striped maple), *Prunus pensylvanica* (pin cherry), and *Sorbus americana* (American mountain ash) (Figure 3); these species models, however, had lower model reliability and are complicated by the geographic influence of the spine of the Appalachian Mountains. Example maps showing the mean centers and their ellipses around current and potential future habitat distributions for two southern species, *Liquidambar styraciflua* L. and *Pinus echinata*, are shown in Figure 4. Fei et al. [78], in an analysis of FIA data across three decades for 86 species/groups in the eastern U.S., found that 62% of species show evidence for a northward shift and that 73% of species show evidence for a westward shift. This westward trend was associated with changes in moisture availability (more moisture now westward) and successional trends (afforestation farther west), though the much sparser FIA data westward into the highly agricultural Midwestern Corn Belt can also contribute to the differences in results with ours. Of the species we have in common ( $n = 78$ ) with the Fei et al. study, our results from the GCM85 scenario show much more potential for northward (87% N, 13% S) over westward (31% W, 69% E) migration of climatically suitable habitat. In future, the GCMs do show a lot more warming northward as compared to the previous 30 years [78,79], and when coupled with a probable constraint of the increased moisture westward [79], these two studies are not incongruent.



**Figure 3.** Potential changes in distance and direction of mean centers of suitable habitat for each of 125 species, according to (a) CCSM45, (b) GCM45, (c) GCM85, and (d) GFDL85. These are the ‘bookends’ of severity (CCSM45 and Had85) and the means (GCM45 and GCM85) of all three models.

**Table 4.** Number of species by distance and generalized northward and southward direction of mean centers of suitable habitat for the 125 species in the eastern United States. Only the ‘bookends’ of severity (CCSM45 and Had85) and the means (GCM45 and GCM85) of all three models are presented.

Scenario	Kilometers							Total
	<10	10–50	51–100	101–200	201–300	301–400	>400	
Northward								
CCSM45	1	16	22	43	10	0	1	93
GCM45	1	12	19	33	19	7	8	99
GCM85	0	9	11	25	23	16	17	101
Had85	0	8	17	22	19	18	16	100
Southward								
CCSM45	0	7	7	10	1	5	2	32
GCM45	0	0	5	9	2	5	5	26
GCM85	0	3	2	6	4	3	6	24
Had85	0	2	4	5	7	2	5	25



**Figure 4.** Ellipses of 1 standard deviation and mean centers for the current distribution and suitable habitat according to CCSM45, GCM45, GCM85, and Had85 under RCP 4.5 (circles) and 8.5 (squares) for (A) *Liquidambar styraciflua* and (B) *Pinus echinata*. Only the ‘bookends’ of severity (CCSM45 and Had85) and the means (GCM45 and GCM85) of all three models are presented. FIA Actual refers to the known FIA plot locations of the species, while Current refers to the modeled current distribution of the species.

Numbers represent the FIA species codes for a few species with potential long distance movements (shown in km): 61 = *Juniperus ashei* J. Buchholz, 315 = *Acer pensylvanicum* L., 404 = *Carya illinoensis* (Wangenh.) K.Koch, 408 = *Carya texana* Buckley, 761 = *Prunus pensylvanica* L.f., 935 = *Sorbus americana*, 973 = *Ulmus crassifolia*.

### 3.4. Analysis of Dominants, Gainers, and Losers by State and Region

In this analysis we identified, for the entire East, five regions, and 37 states plus the District of Columbia, the dominant three species now and what their overall changes are projected for suitable habitat, with 1 meaning no change, <1 meaning a loss in habitat, and >1 meaning a gain in habitat (Table 5). Over the entire eastern U.S., the top three species currently are loblolly pine (*Pinus taeda*), red maple (*Acer rubrum*), and sweetgum (*Liquidambar styraciflua* L.). Of the 36 unique species ranked among the top three positions, those that most frequently scored among the dominant three species

are red maple (for 21 of 44 states or regions), loblolly pine (15 of 44), sugar maple (*Acer saccharum*, 11 of 44), and sweetgum (10 of 44) (Table 5). By genus, the three *Acer* species were found among the top three species 33 times, the five *Pinus* species 25 times, and the nine *Quercus* species 23 times.

For the top three species within the 38 state (and District of Columbia) rankings ( $n = 114$ ), 50 (44%) are expected to lose >10% of their suitable habitat, while 41 (36%) species are projected to gain >10% of habitat by 2100 for the RCP 4.5 scenario; comparable numbers under RCP 8.5 are 58 (51%) losers and 40 (35%) gainers. So, although more of these dominant species are expected to lose habitat suitability in the changed climate, the fact that they are abundant presently and often very adaptable to a changing climate [80,81] increases the probability that many of these species, even the losers, may still be plentiful in their respective states by 2100.

Contrary to the data for the entire suite of 125 species, where 88 species were modeled to gain at least 10% habitat (Table 3), the analysis of only the top three species by state or region shows that a larger number of species are projected to lose habitat as compared to gain habitat (Table 5). Of the 132 iterations of species listed on Table 5 under regions or states, 56 species lost >10% habitat and 51 gained >10% habitat. Primary losers were *Acer rubrum*, *A. saccharum*, *Liriodendron tulipifera* L., and *Populus tremuloides*, while primary gainers were *Pinus taeda* and *Liquidambar styraciflua*.

**Table 5.** Top three species currently in each region and state, along with the future:current ratio of projected suitable habitat under low and high emission scenarios.

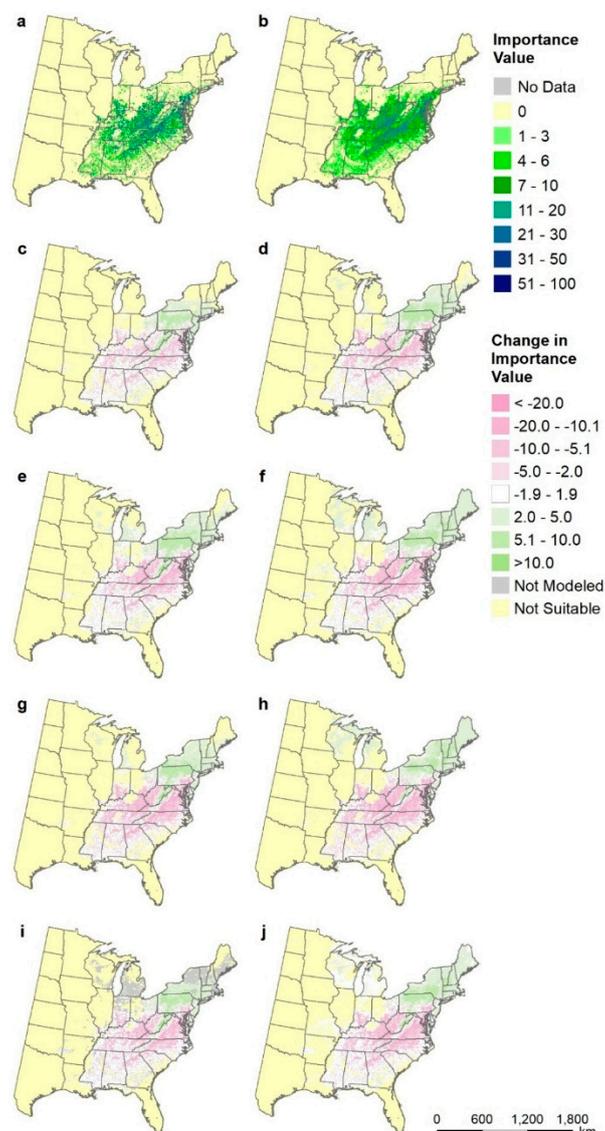
State/Region	First Species	Low	High	Second Species	Low	High	Third Species	Low	High
Eastern U.S.	<i>Pinus taeda</i>	1.21	1.32	<i>Acer rubrum</i>	0.99	0.92	<i>Liquidambar styraciflua</i>	1.48	1.73
Northeast	<i>Acer rubrum</i>	0.91	0.76	<i>Acer saccharum</i>	0.93	0.88	<i>Pinus strobus</i>	1.04	0.87
North Central	<i>Populus tremuloides</i>	0.71	0.61	<i>Acer rubrum</i>	1	0.93	<i>Acer saccharum</i>	1.03	0.98
Great Plains	<i>Ulmus americana</i>	1.44	1.74	<i>Celtis occidentalis</i>	1.53	1.58	<i>Juniperus virginiana</i>	2.64	3.07
Southeast	<i>Pinus taeda</i>	1.07	1.09	<i>Pinus elliotii</i>	1.31	1.42	<i>Liquidambar styraciflua</i>	1.34	1.43
South Central	<i>Pinus taeda</i>	1.2	1.2	<i>Liquidambar styraciflua</i>	1.35	1.42	<i>Quercus stellata</i>	2.15	2.44
Alabama	<i>Pinus taeda</i>	0.98	0.95	<i>Liquidambar styraciflua</i>	1.17	1.21	<i>Quercus nigra</i>	2.04	2.29
Arkansas	<i>Pinus taeda</i>	1.35	1.36	<i>Pinus echinata</i>	1.55	1.56	<i>Quercus alba</i>	0.84	0.82
Connecticut	<i>Acer rubrum</i>	0.7	0.54	<i>Betula lenta</i>	0.65	0.54	<i>Quercus rubra</i>	0.89	0.77
District of Columbia	<i>Liriodendron tulipifera</i>	0.34	0.29	<i>Fagus grandifolia</i>	0.44	0.44	<i>Quercus prinus</i>	0.5	0.49
Delaware	<i>Acer rubrum</i>	0.77	0.69	<i>Pinus taeda</i>	2.38	2.4	<i>Liquidambar styraciflua</i>	1	1.07
Florida	<i>Pinus elliotii</i>	0.93	0.89	<i>Pinus taeda</i>	1.31	1.46	<i>Quercus laurifolia</i>	1.17	1.15
Georgia	<i>Pinus taeda</i>	0.97	0.95	<i>Pinus elliotii</i>	1.19	1.27	<i>Liquidambar styraciflua</i>	1.23	1.29
Iowa	<i>Ulmus americana</i>	1.23	1.27	<i>Juglans nigra</i>	1.39	1.33	<i>Celtis occidentalis</i>	2.24	2.02
Illinois	<i>Ulmus americana</i>	1.29	1.47	<i>Quercus alba</i>	0.92	0.76	<i>Prunus serotina</i>	0.77	0.66
Indiana	<i>Acer saccharum</i>	0.73	0.64	<i>Prunus serotina</i>	0.74	0.6	<i>Fraxinus americana</i>	0.99	0.94
Kansas	<i>Ulmus americana</i>	1.15	1.23	<i>Celtis occidentalis</i>	1.07	1.06	<i>Maclura pomifera</i>	1.21	1.22
Kentucky	<i>Liriodendron tulipifera</i>	0.44	0.35	<i>Acer saccharum</i>	0.66	0.6	<i>Quercus alba</i>	1.01	0.95
Louisiana	<i>Pinus taeda</i>	0.97	0.92	<i>Liquidambar styraciflua</i>	1.13	1.14	<i>Quercus nigra</i>	2.2	2.32
Massachusetts	<i>Acer rubrum</i>	0.81	0.66	<i>Pinus strobus</i>	0.46	0.38	<i>Quercus rubra</i>	1.02	0.92
Maryland	<i>Acer rubrum</i>	0.8	0.72	<i>Pinus taeda</i>	2.32	2.67	<i>Liriodendron tulipifera</i>	0.65	0.47
Maine	<i>Abies balsamea</i>	0.53	0.5	<i>Acer rubrum</i>	1.35	1.24	<i>Picea rubens</i>	0.64	0.57
Michigan	<i>Acer rubrum</i>	0.98	0.87	<i>Acer saccharum</i>	0.82	0.74	<i>Populus tremuloides</i>	0.89	0.8
Minnesota	<i>Populus tremuloides</i>	0.66	0.56	<i>Picea mariana</i>	0.4	0.4	<i>Larix laricina</i>	1.21	1.17
Missouri	<i>Quercus alba</i>	0.57	0.52	<i>Quercus velutina</i>	0.95	0.86	<i>Quercus stellata</i>	1.74	1.94
Mississippi	<i>Pinus taeda</i>	1.09	1.01	<i>Liquidambar styraciflua</i>	1.19	1.2	<i>Quercus nigra</i>	2.05	2.27
North Carolina	<i>Pinus taeda</i>	1.21	1.24	<i>Acer rubrum</i>	0.79	0.77	<i>Liquidambar styraciflua</i>	1.28	1.39
North Dakota	<i>Quercus macrocarpa</i>	1.75	2.58	<i>Populus tremuloides</i>	0.42	0.33	<i>Acer negundo</i>	1.92	1.63
Nebraska	<i>Juniperus virginiana</i>	1.92	2.33	<i>Quercus macrocarpa</i>	1.59	1.57	<i>Ulmus americana</i>	2.1	2.51
New Hampshire	<i>Acer rubrum</i>	1.06	0.91	<i>Pinus strobus</i>	0.79	0.65	<i>Tsuga canadensis</i>	0.77	0.66
New Jersey	<i>Pinus rigida</i>	0.39	0.39	<i>Acer rubrum</i>	1.05	0.92	<i>Quercus alba</i>	1	0.83
New York	<i>Acer rubrum</i>	0.98	0.77	<i>Acer saccharum</i>	0.78	0.71	<i>Fagus grandifolia</i>	0.73	0.67
Ohio	<i>Acer rubrum</i>	0.47	0.4	<i>Acer saccharum</i>	0.89	0.79	<i>Prunus serotina</i>	0.67	0.55
Oklahoma	<i>Quercus stellata</i>	1.09	1.08	<i>Juniperus virginiana</i>	1.24	1.34	<i>Pinus echinata</i>	1.36	1.4
Pennsylvania	<i>Acer rubrum</i>	0.64	0.47	<i>Prunus serotina</i>	0.77	0.63	<i>Acer saccharum</i>	0.91	0.86

Table 5. Cont.

State/Region	First Species	Low	High	Second Species	Low	High	Third Species	Low	High
Rhode Island	<i>Acer rubrum</i>	0.62	0.52	<i>Pinus strobus</i>	0.55	0.42	<i>Quercus rubra</i>	0.72	0.62
South Carolina	<i>Pinus taeda</i>	0.86	0.81	<i>Liquidambar styraciflua</i>	1.08	1.09	<i>Quercus nigra</i>	1.8	2.03
South Dakota	<i>Quercus macrocarpa</i>	5.57	5.65	<i>Juniperus virginiana</i>	5.87	6.93	<i>Fraxinus pennsylvanica</i>	3.75	4.15
Tennessee	<i>Liriodendron tulipifera</i>	0.51	0.42	<i>Quercus alba</i>	1.13	1.08	<i>Acer rubrum</i>	0.81	0.83
Texas	<i>Pinus taeda</i>	0.97	0.9	<i>Juniperus ashei</i>	1.11	1.1	<i>Quercus virginiana</i>	1.49	1.55
Virginia	<i>Pinus taeda</i>	1.45	1.66	<i>Liriodendron tulipifera</i>	0.5	0.33	<i>Acer rubrum</i>	0.82	0.76
Vermont	<i>Acer saccharum</i>	0.61	0.57	<i>Acer rubrum</i>	1.39	1.25	<i>Fagus grandifolia</i>	0.76	0.72
Wisconsin	<i>Populus tremuloides</i>	0.7	0.62	<i>Acer rubrum</i>	0.97	0.8	<i>Acer saccharum</i>	0.94	0.92
West Virginia	<i>Acer rubrum</i>	0.71	0.61	<i>Liriodendron tulipifera</i>	0.84	0.56	<i>Acer saccharum</i>	0.84	0.73

### 3.5. Species-Level Maps

Though putting 10 maps on a page masks fine-scale visualization, it does provide a way to assess the current distribution according to the relatively sparse FIA plots, the modeled current distribution, and the potential future distributions according to each of the model/RCP scenarios, as well as the mean RCP 4.5 and 8.5. For example, *Liriodendron tulipifera* (yellow poplar), a species important for wood products throughout its range (Figure 5) shows a general northward expansion of suitable habitat under warming, with more expansion under RCP8.5 vs. RCP4. The least expansion is with the relatively cool CCSM4 model as compared to the more equivalent Hadley and GFDL models. However, with the driest Hadley model (either RCP4.5 or RCP8.5), habitat for yellow poplar noticeably contracts in the southern third of its current distribution (Figure 5). These maps are available in Figures A1–A3 for three other species, *Pinus echinata* (shortleaf pine) *P. teada* (loblolly pine), and *Liquidambar styraciflua* (sweetgum); all species will eventually be on our atlas website [www.fs.fed.us/nrs/atlas](http://www.fs.fed.us/nrs/atlas).



**Figure 5.** *Liriodendron tulipifera* (yellow poplar) distributions, shown as differences from current modeled distribution (map b): (a) FIA estimate of current distribution of abundance, (b) modeled current distribution, (c) CCSM45, (d) CCSM85, (e) GFDL45, (f) GFDL85, (g) Had45, (h) Had85, (i) mean of all three RCP4.5, and (j) mean of all three RCP8.5.

### 3.6. Comparison to Earlier DISTRIB Models

As expected, there are differences between DISTRIB-II outputs described here from those presented in our earlier work [15]. In our current effort, differences mainly arise from using a hybrid lattice approach, and also from: (1) Newer FIA records, (2) recent 30-year climate normals, (3) a newer set of predictor variables, (4) removal of outlier training data, and (5) modifying predicted IVs with the mean-median combination. The recent FIA records provide information about disturbances and changes in species demographics, while the 30-year climate normals attempt to match conditions experienced by the trees inventoried by FIA. The newer set of environmental predictors incorporates finer scale information (e.g., gSSURGO soils), as well as additional variables not previously used. The removal of outliers from training datasets aims to limit the influence of unrepresentative cells that might result from plantations or severe disturbance events, while the modification of predicted values with the mean-median combination reduced the influence of spurious predictions among the prediction set.

Attributing the differences in results between DISTRIB and DISTRIB-II to any single or combination of the listed factors would be very difficult to quantify and of little practical value to forest managers. Suffice it to say that the newer results are an improvement over the earlier ones. However, as with our earlier results, models with low reliability should be interpreted with caution. As always with modeling studies, ‘all models are wrong’ [82]; we strive to make them useful by making them available to use in concert with any other information and experience available to the decision makers.

## 4. Conclusions

The forests of the eastern United States are characterized by a diverse assemblage of tree species. Climate change has the potential to shift and influence species patterns, thereby creating novel communities, with the greatest disruption and change clearly linked to the emissions pathways that unfold over the course of this century. By quantifying potential habitat changes across a wide array of species over a broad geographic extent, we can consider several dimensions of potential habitat change that lend to understanding individual species responses, as well as focused regional quantification that lend to informed on-the-ground adaptation planning. The trend of increasing general habitat conditions for a large portion of the species is a function of spreading at the range margin extents with, in many cases, a decline in core habitat suitability. Those species projecting losses, while fewer in number, generally show a contraction in the range of suitable habitat under either RCP, but especially so under RCP 8.5. In many cases, a finer extent of regions or state level evaluations reveals the potential impact of shifting habitats via ranked species importance and summary of winners and losers by states or regions. In these more discrete extents, the gradual fading in or out for species presents useful information for planners. Many of the current top species projected to decline in the region (even though their range-wide ratio may be increasing) epitomize the conditions where macro level pressures of climate change can have local level implications. In the end, these results show the high potential for a reshuffling of where suitable habitats for species will occur across the eastern United States, and it is clear that these will reshape competitive pressures and ultimate final outcomes that are beyond any modeling approach. Therefore, we intend these models to be one piece of a package of information that practitioners use for decisions related to adapting to the changing climate we now face. Working together, adaptations in silviculture and ecological management should improve the potential for eastern U.S. forests to continue to thrive in the coming decades.

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## Appendix A

**Table A1.** Importance value  $\times$  area scores (FIAsumIV) and their future:current ratios showing potential gains (light green 1.1–2.0, dark green  $>$  2.0-fold increase) or losses (orange 0.5–0.9, red  $<$  0.5 times decrease) or no change (black 0.9–1.1) under three scenarios of climate change: CCSM4.5, GFDL8.5, Had8.5 and mean of the three models for each RCP (GCM45 and GCM85). Also shown is overall average score (GCMave), and the model reliability for each species.

Scientific Name	Model Reliability	FIA sumIV	CCSM45	GFDL85	HAD85	GCM45	GCM85	GCMave
<i>Abies balsamea</i> (L.) Mill.	High	35,606	0.496	0.504	0.492	0.495	0.506	0.500
<i>Acer barbatus</i> Michx.	Low	1729	1.758	5.877	5.654	3.026	5.277	3.631
<i>Acer negundo</i> L.	Low	25,259	1.356	2.096	1.887	1.637	1.889	1.763
<i>Acer nigrum</i> L.	Low	678	0.409	0.292	0.282	0.364	0.299	0.340
<i>Acer pensylvanicum</i> L.	Medium	2549	0.752	0.565	0.547	0.672	0.580	0.653
<i>Acer rubrum</i> L.	High	165,591	1.030	0.915	0.871	0.993	0.920	0.956
<i>Acer saccharinum</i> L.	Low	14,872	1.804	3.044	2.445	2.309	2.630	2.203
<i>Acer saccharum</i> Marshall	High	88,010	0.945	0.906	0.819	0.932	0.880	0.906
<i>Acer spicatum</i> Lam.	Low	472	0.214	0.177	0.171	0.177	0.164	0.220
<i>Aesculus flava</i> Sol.	Low	1682	0.895	0.666	0.564	0.775	0.682	0.705
<i>Aesculus glabra</i> Willd.	Low	999	0.720	0.588	0.572	0.640	0.584	0.603
<i>Amelanchier</i> spp.	Low	2558	0.956	1.278	1.250	1.024	1.181	1.015
<i>Asimina triloba</i> (L.) Dunal	Low	738	0.488	0.519	0.518	0.495	0.497	0.481
<i>Betula alleghaniensis</i> Britt.	High	17,123	0.828	0.635	0.634	0.753	0.654	0.703
<i>Betula lenta</i> L.	High	13,368	1.029	0.806	0.802	0.966	0.844	0.909
<i>Betula nigra</i> L.	Low	3988	1.632	6.922	8.275	4.053	6.875	4.749
<i>Betula papyrifera</i> Marshall	High	21,096	0.940	0.833	0.779	0.918	0.834	0.876
<i>Betula populifolia</i> Marsh.	Low	1622	1.045	1.293	1.157	1.154	1.191	1.095
<i>Carpinus caroliniana</i> Walter	Low	9337	2.417	4.278	3.472	2.913	3.756	2.954
<i>Carya alba</i> Sarg.	Medium	22,233	1.831	2.998	3.185	2.267	2.920	2.593
<i>Carya aquatica</i> (F.Michx.) Nutt.	Medium	2624	1.278	1.619	1.699	1.380	1.641	1.393
<i>Carya cordiformis</i> (Wangenh.) K.Koch	Low	12,853	1.468	2.757	2.284	1.859	2.315	1.882
<i>Carya glabra</i> Miller	Medium	22,303	1.240	1.494	1.318	1.280	1.401	1.341
<i>Carya illinoensis</i> (Wangenh.) K.Koch	Low	6698	2.613	13.336	15.386	5.479	12.017	7.580
<i>Carya laciniata</i> (Mill.) K.Koch	Low	1009	1.051	1.767	1.080	1.241	1.340	1.177
<i>Carya ovata</i> (Mill.) K.Koch	Medium	19,547	1.149	1.356	1.170	1.281	1.262	1.271
<i>Carya texana</i> Buckley (1861)	High	9390	2.126	6.676	7.545	3.686	6.198	4.358
<i>Celtis laevigata</i> Willdenow	Medium	16,556	2.469	6.786	7.940	3.893	6.580	5.236
<i>Celtis occidentalis</i> L.	Medium	21,798	1.516	2.420	1.974	1.861	2.076	1.968
<i>Cercis Canadensis</i> L.	Low	4198	1.419	3.579	3.607	2.118	3.189	2.353
<i>Chamaecyparis thyoides</i> (L.) B.S.P.	Low	821	1.464	1.927	0.697	1.704	1.542	1.475
<i>Cornus florida</i> L.	Medium	10,589	1.545	1.868	1.631	1.607	1.765	1.554
<i>Diospyros virginiana</i> L.	Low	7074	1.981	8.115	8.345	4.039	7.027	4.814
<i>Fagus grandifolia</i> Ehrh.	High	35,486	1.118	1.291	0.996	1.163	1.193	1.178
<i>Fraxinus Americana</i> L.	Medium	42,548	1.314	1.633	1.547	1.455	1.559	1.507
<i>Fraxinus nigra</i> Marshall	Medium	13,276	1.114	0.934	0.890	1.080	0.955	0.997
<i>Fraxinus pennsylvanica</i> Marshall	Low	47,622	1.872	2.747	2.738	2.200	2.627	2.413
<i>Fraxinus quadrangulata</i> Michx.	Low	631	0.870	1.045	0.709	0.888	0.889	0.827
<i>Gleditsia triacanthos</i> L.	Low	11,912	1.317	3.096	3.083	1.907	2.739	2.078
<i>Gordonia lasianthus</i> (L.) Ellis	Medium	2418	1.666	1.812	1.567	1.651	1.712	1.549
<i>Halesia</i> spp.	Low	150	1.354	1.627	1.314	1.486	1.518	1.391
<i>Ilex opaca</i> Aiton	Medium	5391	1.829	2.456	2.165	2.018	2.304	1.956
<i>Juglans nigra</i> L.	Low	24,037	1.282	2.367	2.081	1.678	2.069	1.873
<i>Juniperus ashei</i> J. Buchholz	High	21,113	1.334	3.632	7.938	1.863	4.673	3.268
<i>Juniperus virginiana</i> L.	Medium	49,834	1.794	3.717	3.864	2.524	3.508	3.016
<i>Larix laricina</i> (Du Roi) K. Koch	High	12,797	1.198	1.170	1.161	1.238	1.215	1.176
<i>Liquidambar styraciflua</i> L.	High	91,344	1.342	1.816	1.802	1.479	1.730	1.604
<i>Liriodendron tulipifera</i> L.	High	63,276	0.895	0.821	0.645	0.807	0.766	0.786
<i>Maclura pomifera</i> (Raf.) Schneid.	Medium	11,988	1.167	2.920	2.610	1.755	2.408	1.883

Table A1. Cont.

Scientific Name	Model Reliability	FIA sumIV	CCSM45	GFDL85	HAD85	GCM45	GCM85	GCMave
<i>Magnolia acuminata</i> L.	Low	1734	1.058	1.106	1.066	1.039	1.086	1.008
<i>Magnolia fraseri</i> Walter	Low	651	1.542	1.667	1.610	1.540	1.653	1.465
<i>Magnolia grandiflora</i> L.	Low	1407	5.634	11.214	3.819	6.490	8.227	6.387
<i>Magnolia macrophylla</i> Michx.	Low	292	0.891	0.979	0.678	0.879	0.889	0.823
<i>Magnolia virginiana</i> L.	Medium	7875	2.622	3.793	1.945	2.798	3.129	2.658
<i>Morus rubra</i> L.	Low	8905	1.432	3.160	1.991	1.955	2.345	1.904
<i>Nyssa aquatic</i> L.	Medium	5014	1.284	1.856	1.215	1.377	1.587	1.360
<i>Nyssa biflora</i> Walter	Medium	14,558	1.716	2.140	1.813	1.816	1.991	1.760
<i>Nyssa sylvatica</i> Marshall	Medium	25,962	1.772	2.576	2.449	2.037	2.450	2.243
<i>Ostrya virginiana</i> (Mill.) K.Koch	Low	12,225	2.107	3.507	2.670	2.599	3.017	2.500
<i>Oxydendrum arboretum</i> (L.) DC.	High	11,224	1.020	0.911	0.701	0.885	0.860	0.877
<i>Persea borbonia</i> (L.) Spreng.	Low	2757	1.729	2.491	1.563	1.839	2.078	1.776
<i>Picea glauca</i> (Moench) Voss	Medium	7764	0.758	0.844	0.863	0.778	0.842	0.807
<i>Picea mariana</i> (Mill.) Britton, Sterns & Poggenburg	High	14,500	0.497	0.468	0.453	0.474	0.460	0.534
<i>Picea rubens</i> Sarg.	High	13,049	0.689	0.556	0.554	0.612	0.555	0.637
<i>Pinus banksiana</i> Lamb.	Medium	9280	0.719	0.635	0.642	0.689	0.661	0.702
<i>Pinus clausa</i> (Chapm. ex Engelm.) Sarg.	Medium	3740	1.223	1.573	0.850	1.413	1.275	1.263
<i>Pinus echinata</i> Mill.	High	32,601	2.147	3.848	3.985	2.796	3.665	3.231
<i>Pinus elliotii</i> Engelm.	High	57,498	1.450	2.093	1.622	1.577	1.858	1.718
<i>Pinus glabra</i> Walter	Low	1039	0.507	0.608	0.297	0.551	0.487	0.533
<i>Pinus palustris</i> Mill.	Medium	19,920	2.677	4.428	2.167	2.933	3.507	3.220
<i>Pinus pungens</i> Lamb.	Low	527	0.798	1.297	1.541	1.061	1.246	1.061
<i>Pinus resinosa</i> Sol. ex Aiton	Medium	17,992	0.945	0.967	0.937	0.998	0.973	0.985
<i>Pinus rigida</i> Mill.	High	5653	0.754	0.948	0.982	0.818	0.928	0.854
<i>Pinus serotina</i> Michx.	Medium	4019	1.471	1.569	1.203	1.335	1.448	1.298
<i>Pinus strobus</i> L.	High	42,529	1.137	0.882	0.827	1.090	0.921	1.006
<i>Pinus taeda</i> L.	High	271,571	1.178	1.404	1.285	1.212	1.324	1.268
<i>Pinus virginiana</i> Mill.	High	21,514	0.915	0.933	0.888	0.843	0.913	0.878
<i>Planera aquatic</i> J.F.Gmel.	Low	932	1.940	3.579	4.961	2.526	3.987	2.854
<i>Platanus occidentalis</i> L.	Low	11,992	1.963	4.698	4.200	2.803	4.053	3.030
<i>Populus balsamifera</i> L.	Medium	5854	0.431	0.314	0.423	0.380	0.385	0.445
<i>Populus deltoides</i> W.Bartram ex Marshall	Low	11,742	1.935	4.570	3.983	2.881	4.034	3.034
<i>Populus grandidentata</i> Michaux	Medium	12,814	1.218	1.034	0.974	1.235	1.074	1.094
<i>Populus tremuloides</i> Michx.	High	54,642	0.814	0.671	0.636	0.775	0.691	0.733
<i>Prunus pensylvanica</i> L.f.	Low	1734	0.354	0.132	0.151	0.284	0.164	0.259
<i>Prunus serotina</i> Ehr.	Medium	60,388	1.380	1.529	1.404	1.477	1.466	1.472
<i>Quercus alba</i> L.	Medium	87,470	1.225	1.364	1.300	1.317	1.330	1.324
<i>Quercus bicolor</i> Willd.	Low	2188	1.833	3.550	2.420	2.713	3.077	2.549
<i>Quercus coccinea</i> Muenchh.	Medium	17,739	1.128	1.221	1.137	1.168	1.208	1.188
<i>Quercus ellipsoidalis</i> E.J.Hill	Medium	6120	1.679	1.915	1.454	1.909	1.733	1.677
<i>Quercus falcate</i> Michx.	Medium	24,747	2.091	3.581	4.291	2.697	3.659	3.178
<i>Quercus imbricaria</i> Michx.	Medium	4356	0.680	0.802	0.516	0.772	0.635	0.704
<i>Quercus incana</i> Bartram	Low	624	1.050	3.781	9.120	2.678	5.097	3.404
<i>Quercus laevis</i> Walter	Medium	2731	1.205	1.590	1.009	1.258	1.327	1.211
<i>Quercus laurifolia</i> Michx.	Medium	15,945	1.947	2.739	1.708	2.046	2.263	1.974
<i>Quercus lyrata</i> Walter	Medium	4159	1.589	3.426	3.826	2.166	3.289	2.435
<i>Quercus macrocarpa</i> Michx.	Medium	19,711	1.705	1.941	1.592	1.859	1.816	1.837
<i>Quercus marilandica</i> Muenchh.	Medium	10,061	2.750	10.400	11.679	5.241	9.588	6.459
<i>Quercus michauxii</i> Nutt.	Low	2156	2.111	3.834	2.445	2.643	3.098	2.531
<i>Quercus muehlenbergii</i> Engelm.	Medium	6459	1.230	2.054	1.388	1.484	1.613	1.433
<i>Quercus nigra</i> L.	High	46,637	2.089	3.282	3.325	2.568	3.195	2.882
<i>Quercus pagoda</i> Raf.	Medium	7681	2.027	3.388	3.255	2.470	3.199	2.539
<i>Quercus palustris</i> Münchh.	Low	4434	0.974	2.846	1.892	1.347	1.970	1.510
<i>Quercus phellos</i> L.	Low	10,282	2.116	3.299	3.727	2.625	3.336	2.653
<i>Quercus prinus</i> Willd.	High	34,675	1.186	1.270	1.177	1.191	1.233	1.212
<i>Quercus rubra</i> L.	Medium	55,330	1.410	1.460	1.337	1.478	1.416	1.447
<i>Quercus shumardii</i> Buckland	Low	2523	1.127	5.424	4.020	2.050	3.989	2.664
<i>Quercus stellata</i> Wangenh.	High	58,812	2.169	4.671	5.252	3.077	4.504	3.791
<i>Quercus texana</i> Buckley	Low	2363	1.282	1.681	1.597	1.361	1.589	1.353
<i>Quercus velutina</i> Lam.	High	44,550	1.598	2.469	2.301	1.962	2.273	2.118
<i>Quercus virginiana</i> Mill.	High	25,609	2.450	7.093	10.064	3.789	7.552	5.670
<i>Robinia pseudoacacia</i> L.	Low	18,414	1.380	3.449	3.471	1.922	3.030	2.476
<i>Sabal palmetto</i> (Walt.) Lodd.	Medium	4949	2.046	3.867	2.557	2.337	3.123	2.473
<i>Salix nigra</i> Marshall	Low	13,959	1.445	4.936	5.616	2.458	4.558	3.075
<i>Sassafras albidum</i> (Nutt.) Nees	Low	14,728	1.477	2.377	2.631	1.871	2.346	1.908
<i>Sideroxylon lanuginosum</i> ssp. <i>lanuginosum</i>	Low	2109	7.622	49.696	89.291	23.994	56.912	34.731
<i>Sorbus Americana</i> Marshall	Low	147	0.397	0.265	0.292	0.334	0.282	0.330
<i>Taxodium ascendens</i> Brongn.	Medium	8177	2.305	4.612	2.979	2.467	3.457	2.646

Table A1. Cont.

Scientific Name	Model Reliability	FIA sumIV	CCSM45	GFDL85	HAD85	GCM45	GCM85	GCMave
<i>Taxodium distichum</i> (L.) Rich.	Medium	8683	2.324	3.622	2.692	2.599	3.131	2.558
<i>Thuja occidentalis</i> L.	High	20,487	0.808	0.854	0.975	0.818	0.926	0.872
<i>Tilia americana</i> L.	Medium	20,151	1.432	1.385	1.196	1.496	1.336	1.416
<i>Tsuga Canadensis</i> (L.) Carrière	High	27,300	1.035	0.724	0.707	0.926	0.765	0.846
<i>Ulmus alata</i> Michx.	Medium	21,303	2.273	4.353	5.729	3.137	4.597	3.867
<i>Ulmus americana</i> L.	Medium	55,590	1.475	2.316	2.401	1.799	2.218	2.008
<i>Ulmus crassifolia</i> Nutt.	Medium	8062	3.431	14.046	23.482	7.557	15.895	10.167
<i>Ulmus rubra</i> Muhl.	Low	13,179	1.359	2.543	2.828	1.774	2.453	1.907

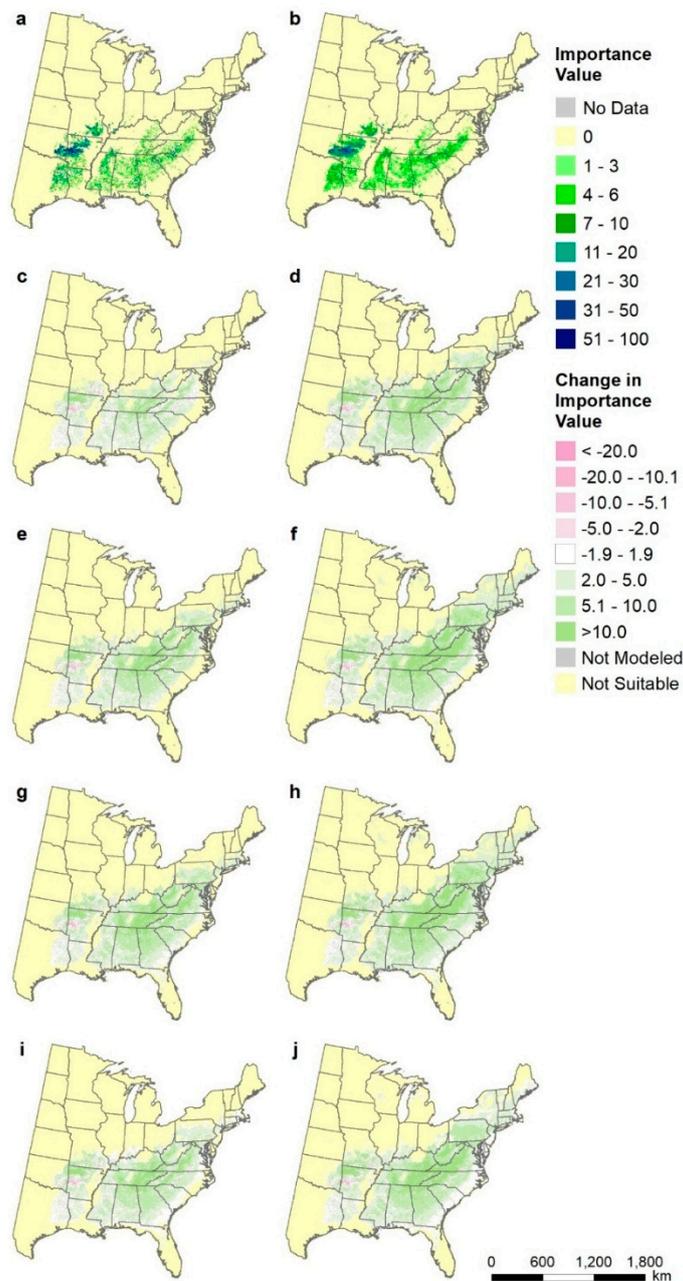
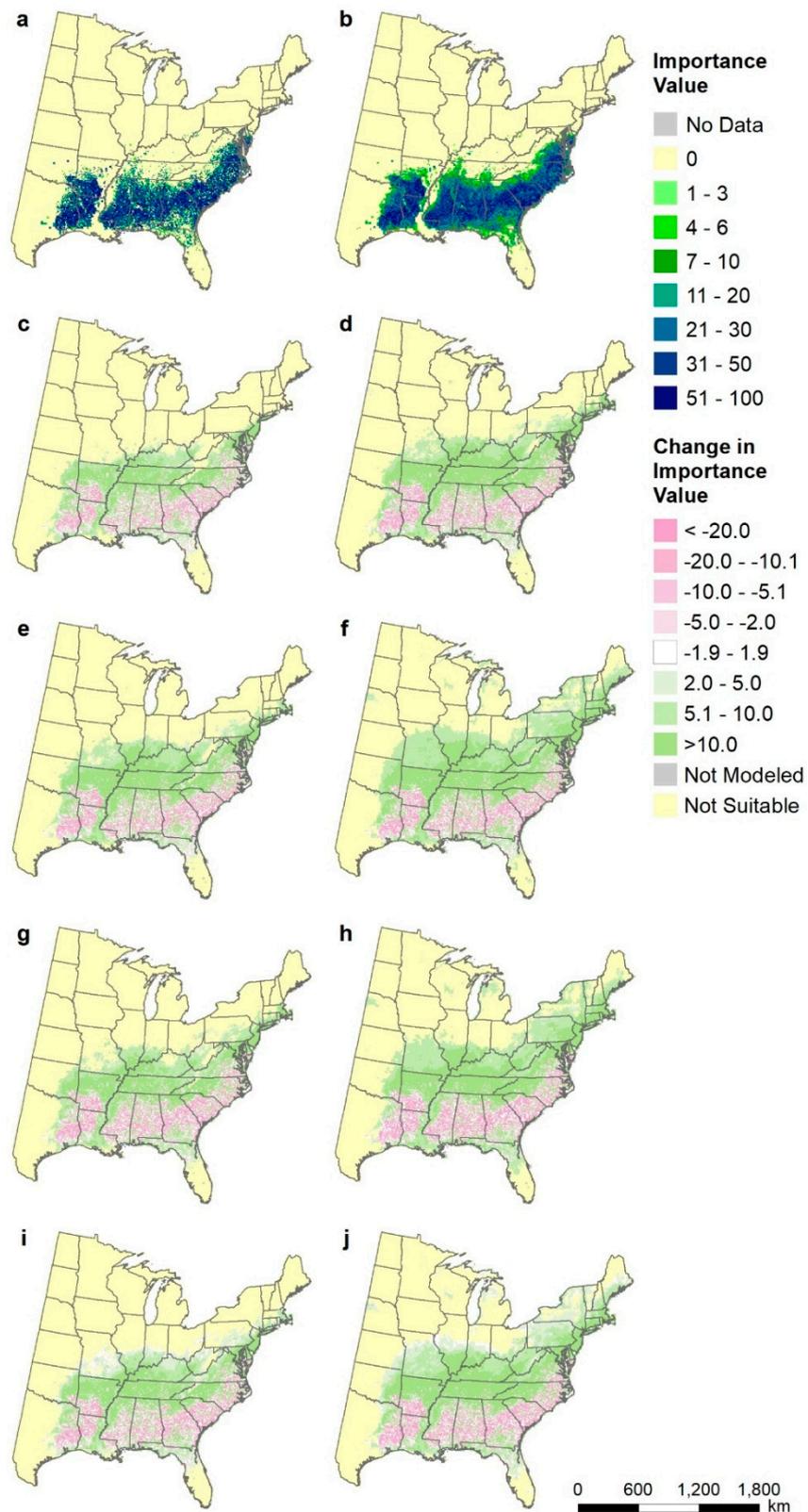
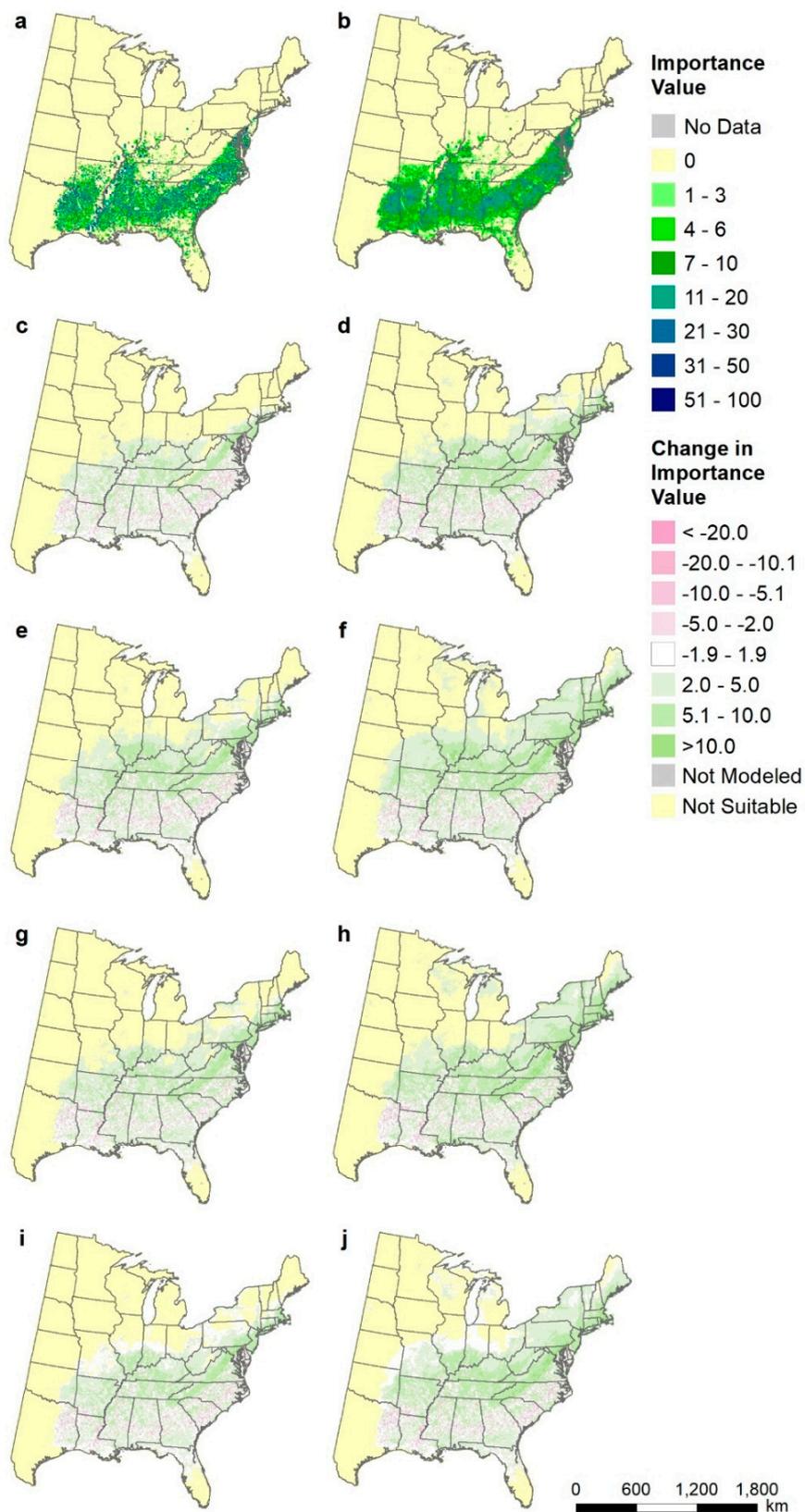


Figure A1. Species distributions for *Pinus echinata* (shortleaf pine), shown as differences from current modeled distribution (map b): (a) FIA estimate of current distribution of abundance, (b) modeled current distribution, (c) CCSM45, (d) CCSM85, (e) GFDL45, (f) GFDL85, (g) Had45, (h) Had85, (i) mean of all three RCP4.5, and (j) mean of all three RCP8.5.



**Figure A2.** Species distributions for *Pinus taeda* (loblolly pine), shown as differences from current modeled distribution (map b): (a) FIA estimate of current distribution of abundance, (b) modeled current distribution, (c) CCSM45, (d) CCSM85, (e) GFDL45, (f) GFDL85, (g) Had45, (h) Had85, (i) mean of all three RCP4.5, and (j) mean of all three RCP8.5.



**Figure A3.** Species distributions for *Liquidambar styraciflua* (sweetgum), shown as differences from current modeled distribution (map b): (a) FIA estimate of current distribution of abundance, (b) modeled current distribution, (c) CCSM45, (d) CCSM85, (e) GFDL45, (f) GFDL85, (g) Had45, (h) Had85, (i) mean of all three RCP4.5, and (j) mean of all three RCP8.5.

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