

# Estimating potential habitat for 134 eastern US tree species under six climate scenarios

Louis R. Iverson\*, Anantha M. Prasad,  
Stephen N. Matthews, Matthew Peters

*US Forest Service, 359 Main Road, Delaware, OH 43015, USA*

Received 13 March 2007; received in revised form 3 July 2007; accepted 15 July 2007

## Abstract

We modeled and mapped, using the predictive data mining tool Random Forests, 134 tree species from the eastern United States for potential response to several scenarios of climate change. Each species was modeled individually to show current and potential future habitats according to two emission scenarios (high emissions on current trajectory and reasonable conservation of energy implemented) and three climate models: the Parallel Climate Model, the Hadley CM3 model, and the Geophysical Fluid Dynamics Laboratory model. Since we model potential suitable habitats of species, our results should not be interpreted as actual changes in ranges of the species. We also evaluated both emission scenarios under an “average” future climate from all three models. Climate change could have large impacts on suitable habitat for tree species in the eastern United States, especially under a high emissions trajectory. Of the 134 species, approximately 66 species would gain and 54 species would lose at least 10% of their suitable habitat under climate change. A lower emission pathway would result in lower numbers of both losers and gainers. When the mean centers, i.e. center of gravity, of current and potential future habitat are evaluated, most of the species habitat moves generally northeast, up to 800 km in the hottest scenario and highest emissions trajectory. The models suggest a retreat of the spruce-fir zone and an advance of the southern oaks and pines. In any case, our results show that species will have a lot less pressure to move their suitable habitats if we follow the path of lower emissions of greenhouse gases. The information contained in this paper, and much more, is detailed on our website: <http://www.nrs.fs.fed.us/atlas>.

Published by Elsevier B.V.

**Keywords:** Climate change; Eastern United States; Tree species distributions; Composition changes; Species shifts; Random Forests; Regression tree analysis; Bagging

## 1. Introduction

Climate change has been shown to affect an increasing number of species across the world (Fitter and Fitter, 2002; Cotton, 2003; Parmesan and Galbraith, 2004; Laliberte and Ripple, 2004; Wilson et al., 2004). Evidence is mounting that these changes will continue to accelerate. Recently there have been many studies that use a modeling approach to predict the effects of future climatic change on ecological systems (e.g., Natl. Assess. Synth. Team, 2001; Yates et al., 2000; Hansen et al., 2001; Retuerto and Carballeira, 2004; Guisan and Thuiller, 2005; Lovejoy and Hannah, 2005; Ibanez et al., 2006; Thuiller et al., 2006; Rehfeldt et al., 2006). A recent study on

the boreal forests of Siberia, Canada, and Alaska reported that many of the modeled predictions of forest change are now occurring: a northern and upslope migration of certain trees, death or dieback of certain species, and increased outbreaks of insects and fire (Soja et al., 2007). The projected increases of atmospheric CO<sub>2</sub> concentration and changes in temperature and precipitation patterns have the potential to alter ecosystem functions, species interactions, population biology, and plant distribution (Melillo et al., 1990; Kirschbaum, 2000). Paleocological evidence also supports the notion that tree species eventually will undergo radical changes in distribution (Davis and Zabinski, 1992; DeHayes et al., 2000).

Groups of species will not shift as intact groups, but rather changes in distribution will occur independently so that the various species that combine to form a community will come together in different combinations under climate change (Webb and Bartlein, 1992). Because of the nature of species

\* Corresponding author. Tel.: +1 740 368 0097; fax: +1 740 368 0152.  
E-mail address: [liverson@fs.fed.us](mailto:liverson@fs.fed.us) (L.R. Iverson).

combinations, it is important to evaluate potential changes in tree species individually rather than through predetermined groups of species or forest types. We used an updated statistical approach to model changes in habitat for 134 individual tree species that are found in the eastern United States.

Our group has been statistically modeling potential change in habitat for common tree species in the eastern United States. We initially developed DISTRIB around regression tree analysis, a procedure of recursive partitioning, to predict the potential future habitat for 80 tree species (Iverson and Prasad, 1998; Iverson et al., 1999a; Prasad and Iverson, 1999). This model was run at the scale of the county and used 33 climatic, edaphic, and land-use variables.

In this more recent effort, we again focus on the eastern United States for the modeling but have made a series of improvements that increase our confidence in the outcomes: (1) the models run at a finer scale of resolution, 20 km × 20 km rather than at the county scale; (2) newer forest inventory data are used; (3) estimates of soil and land use are updated; (4) analysis of model behavior and fit are improved; (5) an additional 54 species are modeled; and (6) an improved modeling tool, Random Forests, is used to develop the models (Iverson et al., 2004a; Prasad et al., 2006). We also ran the models for three new climate scenarios with two emission trajectories each (see Hayhoe et al., 2006).

## 2. Methods

### 2.1. Data

We used the most recent downscaled data for current and future climates, created by Hayhoe et al. (2006) from three general circulation model outputs: the HadleyCM3 model (hereafter abbreviated 'Had') (Pope, 2000), the Geophysical Fluid Dynamics Laboratory ('GFDL') (GFDL CM2.1) model (Delworth et al., 2006), and the Parallel Climate Model ('PCM') (Washington et al., 2000). These three scenarios are among the latest generation of numerical models that couple atmospheric, ocean, sea-ice, and land-surface components to represent historical climate variability and estimate projected long-term increases in global temperatures due to human-induced emissions. Atmospheric processes are simulated in these models at a horizontal resolution of 2.5 × 2 degrees (GFDL), 3.75 × 2.5 degrees (HadCM3) or ~2.8 × 2.8 degrees (PCM). Monthly temperature and precipitation fields were statistically down-scaled from monthly to daily values by Hayhoe et al. (2006) for regions with a resolution of one-eighth degree (Wood et al., 2002). Downscaling entailed the use of an empirical statistical technique that maps the probability density functions for modeled monthly and daily precipitation and temperature for the climatological period (1961–1990) onto those of gridded historical observed data. In this way, the mean and variability of both monthly and daily observations are reproduced by the climate model data. We used data for two emission scenarios: the A1fi (high emissions – which assume that the current emission trends continue for the next several decades without modification, hereafter abbreviated 'hi' when paired with a model

Table 1

Average climate conditions in the eastern US: currently and for four future scenarios: Hadley A1fi, PCM B1, and average A1fi and B1 for Hadley, PCM, and GFDL

Variable	Current	Hadley high	PCM low	Ave high	Ave low
PPT (mm)	1027	1118	1082	1066	1083
PPTMAYSEP (mm)	499	498	536	485	515
TJAN (C)	-0.9	4.7	0.9	3.5	1.5
TJUL (C)	24.0	32.4	26.1	31.4	27.4
JULJANDIFF (C)	25.0	27.6	25.2	27.9	25.9
TMAYSEP (C)	21.1	29.0	23.2	27.9	24.4
TAVG (C)	12.1	19.1	14.2	17.8	15.1

abbreviation) and the B1 (significant conservation and reduction of CO<sub>2</sub> emissions, hereafter abbreviated 'lo'). These two emissions scenarios bracket most of the emission futures as outlined by the Intergovernmental Panel on Climate Change's evaluation of emission scenarios (Nakicenovic et al., 2000), and end the century at roughly double (550 ppm-B1) and triple (970 ppm-A1fi) the pre-industrial levels of CO<sub>2</sub>. We also averaged the three models for each emission scenario to yield an average high (Ave hi) and average low (Ave lo) emission set of climate predictors. We used these two averages plus the PCM B1 (coolest scenario, PCM lo) and HadleyCM3 A1fi (warmest scenario, Had hi) to represent the averages and extremes of possible outcomes from the climate analysis. Average climate data show that all four scenarios predict a warmer and wetter eastern United States (Table 1).

Tree data were obtained from more than 100,000 Forest Inventory and Analysis (FIA) plots for the eastern United States. From these plots (Miles et al., 2001), importance values (IV) for 134 tree species were calculated based equally on the relative number of stems and the relative basal area in each plot (formula in Iverson and Prasad, 1998). Thus, some species with large numbers of medium stems may be calculated as more important than species with fewer, but larger stems. For example, elms (*Ulmus*), maples (*Acer*), and ashes (*Fraxinus*) commonly have very high numbers of small stems and thus may have higher IV values than expected if evaluating only canopy trees. The plot data were averaged to yield IV estimates for each 20 km × 20 km cell for each species. To minimize species that have too few samples to build a respectable model (see Schwartz et al., 2006), species were only included if they were native and had roughly 50 cells or more of occupancy in the eastern United States based on the FIA data (32 species were dropped). As a result, all common and many uncommon species are included, but a few of the rare endemics have insufficient data for modeling with our methods. FIA data also tend to undersample riparian areas as they are usually narrow strips within an upland matrix. Currently, FIA data allow species-by-species analysis only in the United States. The data set for the eastern United States is the most complete, so our work is focused on this region. Other data, including four land-use, one fragmentation, seven climate, five elevation, nine soil classes, and 12 soil property variables, were obtained from various agencies and data clearinghouses to provide the 38 predictor variables (Table 2).

Table 2  
Variables used to predict current and future tree species habitat

Climate <sup>a</sup>	
TAVG	Mean annual temperature (°C)
TJAN	Mean January temperature (°C)
TJUL	Mean July temperature (°C)
TMAYSEP	Mean May–September temperature (°C)
PPT	Annual precipitation (mm)
PPTMAYSEP	Mean May–September precipitation (mm)
JULJANDIFF	Mean difference between July and January temperature (°C)
Elevation <sup>b</sup>	
ELV_CV	Elevation coefficient of variation
ELV_MAX	Maximum elevation (m)
ELV_MEAN	Average elevation (m)
ELV_MIN	Minimum elevation (m)
ELV_RANGE	Range of elevation (m)
Soil class <sup>c</sup>	
ALFISOL	Alfisol (%)
ARIDISOL	Aridisol (%)
ENTISOL	Entisol (%)
HISTOSOL	Histosol (%)
INCEPTSOL	Inceptisol (%)
MOLLISOL	Mollisol (%)
SPODOSOL	Spodosol (%)
ULTISOL	Ultisol (%)
VERTISOL	Vertisol (%)
Soil property <sup>d</sup>	
BD	Soil bulk density (g/cm <sup>3</sup> )
CLAY	Percent clay (<0.002 mm size)
KFFACT	Soil erodibility factor, rock fragment free (susceptibility of soil erosion to water movement)
NO10	Percent soil passing sieve no. 10 (coarse)
NO200	Percent soil passing sieve no. 200 (fine)
OM	Organic matter content (% by weight)
ORD	Potential soil productivity (m <sup>3</sup> timber/ha)
PERM	Soil permeability rate (cm/h)
PH	Soil pH
ROCKDEP	Depth to bedrock (cm)
SLOPE	Soil slope (%) of a soil component
TAWC	Total available water capacity (cm, to 152 cm)
Land use and fragmentation <sup>e</sup>	
FRAG	Fragmentation index (Riitters et al. (2002))
AGRICULT	Cropland (%)
FOREST	Forest land (%)
NONFOREST	Nonforest land (%)
WATER	Water (%)

<sup>a</sup> From Hayhoe et al. (2006). See text for further description.

<sup>b</sup> From the United States Geological Survey's Digital Elevation Models built from 1:100,000 scale maps, and produced at the 30 m × 30 m resolution (U.S. Geological Survey, 1990). We calculated the five elevation variables for each 20 km × 20 km cell based on the 30 m elevation cells contained within the 20 km × 20 km cell.

<sup>c</sup> From Olson et al. (1980). These estimates, made by Olson et al. to the county level from the Soil Conservation Service's National Resources Inventory of 1977, were area-weighted resampled to each 20 km × 20 km cell.

<sup>d</sup> From the Natural Resource Conservation Service's STATSGO data (Soil Conservation Service, 1991). STATSGO data contain physical and chemical soil properties for about 18,000 soil series in the United States. The maps were compiled by generalizing more detailed soil-survey maps into soil associations at a scale of 1:250,000. Weighted averages by depth and by area were calculated for each 20 km × 20 km cell.

<sup>e</sup> From Riitters et al. (2002). Riitters et al. prepared the database from 30 m × 30 m classified Landsat data; we aggregated the land-use data to 20 km × 20 km cells, and calculated the fragmentation index for each cell according to the methods described in Riitters et al. (2002).

## 2.2. Modeling

We used a tri-model approach to model each species: Regression Tree Analysis (RTA), Bagging Trees (BT), and Random Forests (RF). The purpose of such an approach is to make the best data set available for interpretation (RTA), reliability assessment (BT), and prediction (RF). RTA builds a regression tree based on a set of decision rules for the predictor variables by recursively partitioning the data into successively smaller groups with binary splits based on single predictor variables (Breiman et al., 1984; Therneau and Atkinson, 1997). RTA was used in our earlier work (Iverson and Prasad, 1998) as it showed clear advantages over general linear models. We continue to use RTA as a valuable interpretive tool for models with high reliability (see next section). However, it may generate an unstable output where a small change in a predictor variable occasionally may produce a large change in predicted output. This is where BT and RF have advantage. Multiple training sets obtained by resampling 67% of the data with replacement create an average output that is much more stable. In this study, we use BT to produce 30 bootstrapped regression trees (Breiman, 1996) and RF to produce 1000 regression trees (Breiman, 2001), documented in Prasad et al. (2006).

RF is similar to BT in that samples are drawn to construct multiple trees; however in RF, each tree also is grown with a randomized subset of predictor variables (in our case, 15 of the 36 variables were randomly selected for each perturbed tree). The large number of trees (1000 in our case) are grown (hence a "forest" of trees) and averaged to yield more accurate predictions as compared to other RTA or BT (Prasad et al., 2006). We used the "out of bag" outputs from RF (37% of the data that are not used for the individual regression tree-model building) so that the resulting RF models do not overfit the data. Our previous work and that of others have shown that RF provides reasonable outcomes when faced with predicting into novel parameter space (see Prasad et al., 2006).

In all our tests, we have been pleased with the capabilities of RF to empirically model species current and future habitats. The modeled current outputs typically produce a very good wall-to-wall surface from the relatively sparse point data, as shown by various spatial metrics used to evaluate the models' predictive properties by us and others (Iverson et al., 2004a; Prasad et al., 2006; Rehfeldt et al., 2006). However, we also recognize that there are certainly limitations to this or any modeling approach. In this approach, we cannot include changes in land use and land cover likely to occur in the next 100 years, or disturbances such as pests, pathogens, natural disasters, and other human activities. Coupling these outputs with process-based ecosystem dynamics models which include disturbance (e.g., Chaing et al., 2006; Cushman et al., 2007; Scheller et al., 2007) would be a productive line of research.

## 2.3. Model reliability assessment

We developed a reliability rating for the models of each species because not all species can be modeled to the same degree of accuracy using the same model. In addition to the

pseudo  $R^2$  of the RF model, we generated additional reliability indicators based on the BT analysis and combined them for a final rating. Because we have 30 model outcomes from BT, we can use the variability among these 30 outcomes to assess the consistency of the results. With a stable model, the deviance explained would vary little across trees; an unstable model would yield trees explaining varying degrees of deviance. The CVbag variable (coefficient of variation of BT outcomes) was calculated by: (1) taking the weighted sums of the predictor importance of each of the top five predictors; (2) calculating the coefficient of variation (0–1) among the 30 outcomes from BT (all outcomes had standard deviations less than the mean); and (3) subtracting this value from 1 to obtain a 0–1 score with 1 being most stable. Thus, it considers the amount and consistency of contribution of the top five predictors. The Top5 variable uses the rank order of the top five predictors to compare between the top five RF variables vs. the top five variables of each of the 30 BT outputs. We chose five variables arbitrarily to represent the primary drivers. This is another 0–1 scale with 1 indicating that all five variables match the order exactly between RF and a bagging output. Conversely, a 0 indicates a completely different set of top five variables.

The Fuzzy Kappa variable is based on a cell-by-cell comparison between the actual FIA map and the modeled current map derived from the out-of-bag RF environmental predictor data (see Prasad et al., 2006), again on a 0–1 scale with 1 being a perfect match. Kappa and Fuzzy Kappa are better measures than percentage correct (which are always in the 90+ percentile) because the Kappa statistics account for uneven quantities of classes (Hagen-Zanker et al., 2006). The “fuzzy” part of the Kappa takes into consideration that classes closer together, i.e., IV 1–3 vs. IV 4–6, should be considered a closer match than classes farther apart, i.e., IV 0 vs. IV 21–30. The final model reliability score was calculated as the average ( $R^2*2$ , CVbag, Top5IV, FuzKap) with a double weight for  $R^2$  because it is the most direct measurement of model fit. We classified these into three arbitrarily chosen classes: green (reliable, score > 0.5), amber (moderately reliable, score > 0.3 and < 0.5), and red (poor reliability, score < 0.3). We also indicate the portion of the current range that is within the United States (based on Little, 1971, 1977) because if the species is primarily a Canadian species, there will be less confidence in the model as well (because models are built with FIA data from the U.S. only). These also were coded green (>67% in U.S.), amber (33–67%) and red (<33% in U.S.).

#### 2.4. Analysis

With 134 species, three scenarios, two emission pathways, and multiple ways to analyze the data, we selected a subset of these results for this paper (full range of outcomes, plus the averages), which allows an overview of potential impacts of climate change on the eastern U.S. forests. Additional analysis and species-by-species results and maps for all scenarios can be found at <http://www.nrs.fs.fed.us/atlas>.

#### 2.4.1. Evaluation of predictor importance

We developed an index of variable importance (VarImpIdx) to rate the 38 predictors for overall, collective importance as driving variables in models for the 134 species. The index was calculated as the average of three normalized (0–100) scores: (1) the sum of predictor importance scores across all species (SumVarImp); (2) the sum of the reciprocal of rank of each predictor across all species (SumRankRecip); and (3) the frequency of the predictors ranking in the top 10 of importance across all species (FreqTop10).

#### 2.4.2. Percentage occupancy and change in percentage of the region occupied

This tabulation allows a quick assessment of the species that likely would have gains or losses in the *area* of suitable habitat. We divided it into species gaining at least 10% new suitable habitat in the eastern U.S., species gaining 2–10%, no change, and species losing 2 to 10 or >10% of the area.

#### 2.4.3. Area-weighted importance values

This statistic incorporates both area and the relative abundance of each species, so it is a better indicator of suitable habitat gains or losses. Because all cells occupy the same area (400 km<sup>2</sup>), it is simply a sum of the IV values for all pixels in the area of interest. A species may gain area but become so minor that the overall importance of the species is diminished in the study area. In this case, we took the ratio of future to present modeled condition to calculate change: a value <1 indicates a decrease in area-weighted importance and a value >1 indicates an increase.

#### 2.4.4. Changes in mean center of spatial data

ArcGIS 9<sup>1</sup> includes spatial statistic tools for measuring geographic distributions. We used the function Mean Center to calculate the current and future “center of gravity” of the species ranges. The coordinates of the mean center were used to calculate distance and direction of potential movement of the suitable habitat. We used the Direction Distribution function to generate ellipses that captured one standard deviation of the data for visual purposes. Analysis of mean center distance and direction yielded information on potential changes in suitable habitat by species and by scenario. Viewed together in a polar graph, one can see the clustering of distance and direction of movement of suitable habitat.

#### 2.4.5. Analysis of dominants, gainers, and losers by region and state

We used the area-weighted importance value variable to assess current species dominance in the entire eastern United States, in five regions, and in 37 states and the District of Columbia. Because we used the 100th meridian as our western

<sup>1</sup> The use of trade, firm, or corporation names in this paper is for the information and convenience of the user. Such does not constitute an official endorsement or approval by the U.S. Department of Agriculture or Forest Service of any product or service to the exclusion of others that may be suitable.

boundary (an arbitrary line through the prairie states which divides western and eastern U.S. forests), several states in this western region are cut off approximately midway (North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, Texas). Because they are prairie states, few forested regions are missed with the notable exception of the Black Hills of western South Dakota. We scored each species and selected the top three species currently for each state or region. Then we calculated the potential change in this value under the average climate model for low (Ave lo) and high (Ave hi) emissions. The entire species lists are available online, along with the top 10 gainers and top 10 losers for each spatial unit.

#### 2.4.6. Species-level maps

We produced a page of six maps for each species. The maps are: the FIA estimate of current distribution of abundance, the modeled current map, and scenarios of PCM lo, Ave lo, Ave hi, and Had hi. These maps captured the range of possible future conditions according to the models used. Two species have maps sets included in this publication with an additional six species as supplements to this article online. All species can be viewed at our website, <http://www.nrs.fs.fed.us/atlas>.

#### 2.4.7. Forest-type mapping

By combining the individual species into groups of species according to the USDA Forest Service's classification of forest types (Miles et al., 2001), we are able to make some assessments of the potential changes in suitable habitat at the forest-type level. The species' importance values for the selected species within a forest type were summed. For each 20 km × 20 km cell, the forest type with the highest sum was then coded as that forest type in the resulting maps. These calculations were conducted for current and future scenarios.

#### 2.5. Scope and limitations

Our modeling and analysis should be interpreted in the context of data limitations and our assumptions. It should be stressed that we are not trying to model the actual future distributions as that would be beyond the scope of our study. Our models show how future potential suitable habitats could change if climate were to change according to the GCM models. These changes in suitable habitat would impact primarily the regeneration, rather than mature growth, phase of a tree's life cycle. It should be borne in mind that we are modeling the potential niche space that would be available for the species in the future climates, and not the realized niche. Therefore any disturbances would be operating within this future suitable habitat. It should also be noted that the FIA data that we use are integrating the results of past disturbances and climate events, and are thus based on at least a partial realized niche for individual species. Because of genetic plasticity and potential changes in the biotic controls on species ranges, species could expand northward (or southward) even without climate change. Comprehensive modeling of the realized niche would require data on future disturbances, including fires, exotics, severe storms, and human-induced land-use and land-management changes, as well as mortality, growth, and

competition for each species – all out at least 100 years which of course is impossible to achieve. Indeed, the spatial and temporal patterns of these factors are impossible to predict even under the current climate regime, though simulations using the variation of historical data can provide coarse-level indications of potential future conditions, at least for fire (Keane et al., 2004; Cary et al., 2006; Scheller and Mladenoff, 2007). However, it will never be possible to predict major events such as the invasion of the next emerald ash borer, recently introduced and threatening all native ashes (*Fraxinus* spp.) on the continent (Iverson et al., in press-a). Under future altered climates, these factors can manifest themselves in novel and unexpected ways; our models (nor any model), therefore, cannot take these into account. However, the potential future habitats that we do model for each species can be used to investigate further the effect of possible outcomes with respect to modeled disturbances or competition. For example, we have built a spatially explicit cellular model with built-in stochasticity called SHIFT to examine the effects of habitat fragmentation on the future colonization probabilities using the outputs of our models (Iverson et al., 1999b, 2004c,d). It is also possible to combine simulation modeling of future species dynamics with the potential future niche space for various species from our model to achieve a realistic species list that can be modeled forward (e.g., Chaing et al., 2006). Finer scale studies can also be conducted to test our model for species of interest in places where our model is predicting drastic changes (e.g., hotspots).

Therefore, our predictions of increase in range (potential future suitable habitat) are very likely to be overestimates of the actual ranges that would be achieved by the end of this century, as migration of most species will not keep up with relatively abrupt changes in climate, unless humans get seriously involved in moving species.

The RF model is a highly robust model for predictions as it uses thousands of trees with resampled data and randomized subset of predictors. As we have emphasized in our modeling section, this makes it highly resistant to overfitting. However, there is concern that when modeling the future climate by swapping the current with the GCM predicted future, we are sometimes making predictions into novel parameter space through extrapolation. Our investigations into the nature of RF predictions (Prasad et al., 2006) and the fact that RF uses tree-based step-functions rather than splines (e.g., models using adaptive splines such as general additive models or multiple adaptive regression splines) gives us confidence that our extrapolations are not wild projections in future parameter space but are suitably constrained by the robustness of our current modeled response. We do provide model reliability estimates using a tri-model approach (see next section on model reliability) for identifying problematic species.

### 3. Results

#### 3.1. Model reliability assessment

In general, we found high (>0.5) model reliability scores for the most important species. If the data were abundant, the

models usually were reliable according to our rating scheme. Most of the species undergoing the greatest reduction in habitat also were in the green (reliable) zone, while many of the species making an increase in suitable habitat from a low level had a lower reliability rating because of fewer samples from where it is now located.

Results of this assessment show different degrees of reliability, ranging from 0.07 with *Salix amygdaloides* to 0.75 with *Abies balsamea* (Supplement 1). According to our rating scheme, 31 species are in the red (poor reliability) zone,

49 are in the amber (moderately reliable) zone, and 55 are in the green (reliable) zone. We marked these reliability colors on the maps of suitable habitat to help ensure that model reliability is considered when viewing the results. Many of the poor-reliability species are small ranged, that is, the model may have failed to capture the underlying drivers and spatial pattern. This phenomenon was identified and analyzed with respect to forecasting extinctions by Schwartz et al. (2006). There also are 13 species in the red zone due to the low proportion of their current range existing within the eastern United States, and

Table 3  
Assessment of variable importance across all 134 species

	SumRankRecip <sup>1</sup>		FreqTop10 <sup>2</sup>		SumVarImp <sup>3</sup>		VarImpIndx <sup>4</sup>
	Score	Scaled	Score	Scaled	Score	Scaled	Overall score
<b>Climate</b>							
TAVG	6.5	22.8	42	44.7	1828.2	75.5	47.6
TJAN	6.7	23.7	42	44.7	1838.3	75.9	48.1
TJUL	9.2	35.5	47	50.0	1921.9	79.4	54.9
TMAYSEP	11.2	45.1	40	42.6	1825.5	75.4	54.3
PPT	14.6	61.6	73	77.7	2143.8	88.6	76.0
PPTMAYSEP	22.5	100.0	94	100.0	2416.7	100.0	100.0
JULJANDIFF	6.9	24.8	37	39.4	1731.0	71.4	45.2
<b>Elevation</b>							
ELV_CV	5.6	18.4	39	41.5	1728.2	71.3	43.7
ELV_MAX	7.8	28.8	51	54.3	1817.5	75.0	52.7
ELV_MEAN	8.4	31.6	50	53.2	1856.9	76.7	53.8
ELV_MIN	6.8	24.2	37	39.4	1765.3	72.9	45.5
ELV_RANGE	7.9	29.5	48	51.1	1874.7	77.4	52.6
<b>Soil type</b>							
ALFISOL	7.5	27.3	32	34.0	1628.7	67.2	42.8
ARIDISOL	1.8	0.0	0	0.0	16.8	0.0	0.0
ENTISOL	4.3	12.1	10	10.6	1259.3	51.8	24.8
HISTOSOL	3.5	8.1	7	7.4	921.8	37.7	17.8
INCEPTIS	4.6	13.5	25	26.6	1576.0	65.0	35.0
MOLLISOL	10.4	41.2	39	41.5	1660.4	68.5	50.4
SPODOSOL	3.6	8.5	6	6.4	819.6	33.5	16.1
ULTISOL	6.0	20.4	33	35.1	1574.5	64.9	40.1
VERITSOL	2.4	2.8	3	3.2	446.0	17.9	8.0
<b>Soil properties</b>							
BD	2.4	2.7	2	2.1	971.0	39.8	14.9
CLAY	6.9	24.7	50	53.2	1864.7	77.0	51.6
KFFACT	7.5	27.3	13	13.8	1230.7	50.6	30.6
NO10	9.7	38.3	46	48.9	1886.7	77.9	55.0
NO200	11.3	46.0	53	56.4	1959.0	80.9	61.1
OM	4.7	13.8	19	20.2	1560.6	64.3	32.8
ORD	13.3	55.7	63	67.0	2090.4	86.4	69.7
PERM	5.9	19.7	35	37.2	1749.2	72.2	43.1
PH	6.5	22.5	41	43.6	1782.7	73.6	46.6
ROCKDEP	5.1	15.9	31	33.0	1631.3	67.3	38.7
SLOPE	17.6	76.2	76	80.9	2180.8	90.2	82.4
AWC	4.9	15.1	27	28.7	1707.9	70.5	38.1
<b>Landscape</b>							
FRAG	2.4	2.7	0	0.0	875.9	35.8	12.8
AGRICULT	11.0	44.5	55	58.5	1947.6	80.5	61.2
FOREST	11.8	48.4	59	62.8	1969.0	81.3	64.2
NONFOR	5.5	17.6	20	21.3	1575.5	64.9	34.6
WATER	2.6	3.9	5	5.3	502.8	20.3	9.8

Variable names are described in Table 2. Score indicates actual score, while Scaled indicates scores scaled on 0–100 basis. SumRankRecip<sup>1</sup> = sum of the reciprocal of rank of each predictor across all species. FreqTop10<sup>2</sup> = frequency of the predictors ranking in the top 10 of importance across all species. SumVarImp<sup>3</sup> = sum of predictor importance scores across all species. VarImpIndx<sup>4</sup> = Variable Importance Index is overall importance as driving variables in models for the 134 species.

another eight in the amber zone. We did not detect a relationship between the percentage within the eastern United States and the model reliability score.

### 3.2. Predictor importance analysis

The three indices that made up our overall index, VarImpIdx, were all highly correlated to each other (Pearson correlation = 0.77–0.98), so that we can be confident that the index relates well to the importance of these predictors as drivers for species distributions of the 134 trees studied (Table 3). Fortunately, the RF procedure is not hampered by inclusion of correlated predictors as it is in general linear regression modeling (Breiman, 2001). The primary single driving predictor is growing season precipitation (PPTMAY-SEP). This is not a surprising result as trees respond to variations in available moisture, and that moisture is mostly the result of rainfall that falls in the growing season. Second is SLOPE, the average amount of slope in any 20 km × 20 km cell. It is indicative of dissected landscapes, such as is common in the Appalachians and its foothills. It is correlated ( $r = 0.54$ ) with ELV\_RANGE, the variation in elevation within a cell. Because species can move up slope as well as northward in a warming climate, this indicator is important for a number of species centered on the Appalachians. Next is PPT, emphasizing the importance of precipitation, followed by ORD, a soil productivity predictor. ORD probably integrates many of the other soil property predictors into a value correlated with overall capacity of the soil to grow trees, but is most correlated in the eastern U.S. to PPT ( $r = 0.75$ ). Next in importance are FOREST and AGRICULT, which are negatively correlated ( $r = -0.87$ ) because for most cells, if not in agriculture, the area is mostly forested. If an area has survived to date in forest, it is probably well suited for forest (and not as suitable to other land uses), and thus this variable is a good driver for many species. Next in importance are two texture variables, NO200 and NO10. NO200 indicates fine material and is correlated with KFACT ( $r = 0.65$ ) and CLAY ( $r = 0.71$ ), while NO10 indicates coarse textured soils, and is not correlated ( $r < 0.5$ ) with other variables.

The predictors ranked 9 and 10 in importance are the temperature predictors, TJUL and TMAYSEP. However, we believe that temperature, when considered collectively, ranks first or second next to precipitation in importance across all species because of the high correlation among temperature-related variables. For example, TJUL and TMAPSEP are very highly correlated ( $r = 0.98$ ), and TJAN and TAVG are also highly correlated with these two ( $r > 0.9$ ). It is likely that the high correlation among temperature predictors lead to substitution among the four predictors in the models so that the overall importance for a single variable is diminished relative to other, lesser correlated predictors. Thus the ranking of the temperature predictors are lower than if we had included only one or two in the models. Indeed, many species clearly have a temperature variable as their primary driver, but this driver role is shared among four temperature-related variables so

that none emerge on top of the predictor list. Though the RF technique allows the incorporation of correlated variables into the models, a disadvantage is that a clear ranking of the contributing factors is somewhat masked by the substitutions among related variables.

Three elevation predictors follow next in importance (ELV\_MEAN, ELV\_MAX, ELV\_RANGE). The mean and maximum are very highly correlated ( $r = 0.98$ ), but not range. Therefore as with temperature, part of the lower ranking for mean and maximum may be attributed to their substitution capability within the models. After these elevation predictors follows percentage CLAY, a soil texture predictor that relates to tree growth for certain species and then percent MOLLISOL, a typically deep prairie soil common in the western part of the region and the first soil type predictor appearing. When MOLLISOL is high, it forms the western border of a number of eastern tree species.

At the bottom of the list of predictors are six of the soil types, BD, and FRAG. These predictors do not distinctively separate many species of trees because of rarity (e.g., ARIDISOL, WATER, ENTISOL) or their widely dispersed nature (e.g., BD, FRAG).

Table 4

Summary of decreasing and increasing species' area of suitable habitat by scenario for (a) all species of the eastern United States, (b) species bounding Canada, and (c) species not bounding Canada. Scenarios refer to model (PCM, GFDL, Hadley, and average of 3 models) and emission level (low vs. high)

Scenario	Decrease >10%	Decrease 2–10%	No change	Increase 2–10%	Increase >10%	Total
(a)						
PCM lo	0	21	49	48	16	134
PCM hi	2	18	35	27	52	134
Ave lo	0	21	45	37	31	134
Ave hi	2	19	39	23	51	134
GFDL lo	0	19	46	32	37	134
GFDL hi	1	15	36	22	60	134
Had lo	1	21	39	37	36	134
Had hi	3	19	34	24	54	134
(b)						
Bounding Canada						
PCM lo	0	19	19	24	7	69
PCM hi	2	18	14	11	28	73
Ave lo	0	19	20	19	15	73
Ave hi	2	17	19	7	28	73
GFDL lo	0	17	19	16	20	72
GFDL hi	1	11	17	8	36	73
Had lo	1	20	20	16	16	73
Had hi	3	19	17	7	27	73
(c)						
Not bounding Canada						
PCM lo	0	2	30	24	9	65
PCM hi	0	0	21	16	24	61
Ave lo	0	2	25	18	16	61
Ave hi	0	2	20	16	23	61
GFDL lo	0	2	27	16	17	62
GFDL hi	0	4	19	14	24	61
Had lo	0	1	19	21	20	61
Had hi	0	0	17	17	27	61

See text for details.

### 3.3. Estimates and changes in area of suitable habitat

RF model outputs yielded estimates of percentage of the area for each of 134 species, as modeled for the current time, and for year 2100 according to the three models, and their averages, under both low and high emission scenarios (Table 4, Supplement 2). Over all scenarios, we find that more than half (55% on average) of the species show increases in suitable habitat by at least 2% of the total area in the eastern U.S., while only 14% show decreases of at least 2% (Table 4). This might be expected because of the large number of species occupying the southern half of the United States (often with climatic pressure to move north) and a lesser number across the northern tier. According to this assessment, the GFDL hi has the most species gaining area (82, or 61%), while the PCM lo had the lowest percentage of species (64, or 48%) modeled to increase. On the other hand, all scenarios showed only 19–22 species (14–16%) that could decrease by at least 2% (Table 4). Note that 73 of the 134 species currently bound Canada (Table 4, Supplement 2), so a full assessment of the potential change in suitable habitat is not possible, i.e., only habitat within the United States was analyzed. Our data show that almost all of the decreasing species bound Canada; many of these species would find additional suitable habitat in Canada (McKenney et al., 2001). Of those not bounding Canada, 62 of them (46%) are modeled to increase in suitable habitat, and only 0–4 species would decrease at all. Most of the increasing species do not yet reach the Canadian boundary because they are more southern in nature. In either case, the northward shifting of habitat is responsible for these patterns.

Our models indicate that two rare species may lose all suitable habitat in the eastern U.S. under the high emission scenarios: *Quercus durandii* (Durand oak) and *Sorbus americana* (American mountain ash, Supplement 2). Several other species would have severely diminished habitat, especially under the harsher scenarios: *Picea mariana* (black

Table 5

Potential species changes in area-weighted importance value for habitat suitability for 134 species in the eastern United States

Scenario	<0.5	0.5–0.9	0.9–1.1	1.1–2	>2	Total
PCM lo	14	37	21	54	8	134
PCM hi	25	25	14	40	30	134
Ave lo	15	38	20	48	13	134
Ave hi	23	35	9	37	30	134
GFDL lo	14	40	15	44	21	134
GFDL hi	26	28	12	31	37	134
Had lo	20	34	13	50	17	134
Had hi	25	31	12	36	30	134

Allowing for a 10% buffer around 1.0, a future: current ratio below 0.9 indicates a loss, while a value above 1.1 indicates a gain. Scenarios refer to model (PCM, GFDL, Hadley, and average of three models) and emission level (low vs. high). See text for details.

spruce), *Acer spicatum* (mountain maple), and *Juglans cinerea* (butternut).

### 3.4. Species importance values weighted by area

We believe that a calculation that simultaneously includes species area and species importance yields a better indicator of potential change in overall species habitat under various scenarios of climate change. To evaluate, we calculated the ratios of future to current area-weighted importance value for each species and scenario, then classified them for easy interpretation (Table 5, Supplement 3). Averaged across all scenarios, 66 species showed increases, 54 showed decreases, and 14 had no change as compared to the current modeled distribution (Table 5). As such, the inclusion of importance value into the calculations increases the number of decreasing species relative to the area-only evaluation. Many species may not be eliminated entirely but would have a large reduction in suitable habitat. Some of the hardest-hit species under this evaluation include the five species mentioned above plus

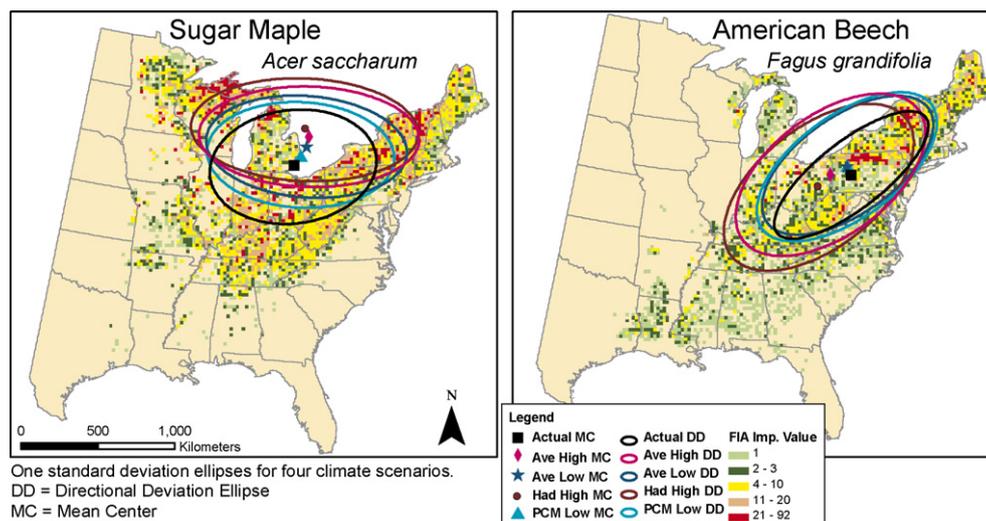


Fig. 1. Ellipses of 1 standard deviation for (a) *Acer saccharum* (sugar maple) and (b) *Fagus grandifolia* (American beech) along with mean centers for the current distribution and suitable habitat according to scenarios of Parallel Climate Model – low emissions (PCM lo), average of three models – low emissions (Ave lo), average of three models – high emissions (Ave hi), and HadleyCM3 model – high emissions (Had hi).

Table 6  
Summary of distance and general north and south direction of mean centers of suitable habitat for the 134 species in the eastern United States

Scenario	Kilometers							Total
	<10	10–50	51–100	101–200	201–300	301–400	>400	
<b>Northward</b>								
PCM lo	4	23	32	37	11	4	0	111
Ave lo	4	18	29	30	18	12	3	114
Ave hi	1	7	16	28	16	10	21	99
Had hi	0	9	16	20	18	10	26	99
<b>Southward</b>								
PCM lo	2	10	4	4	1	1	1	23
Ave lo	1	7	5	3	3	0	1	20
Ave hi	1	6	9	11	4	2	2	35
Had hi	1	6	7	11	7	2	1	35

Scenarios refer to model (PCM, Hadley, and average of three models) and emission level (low vs. high). See text for details.

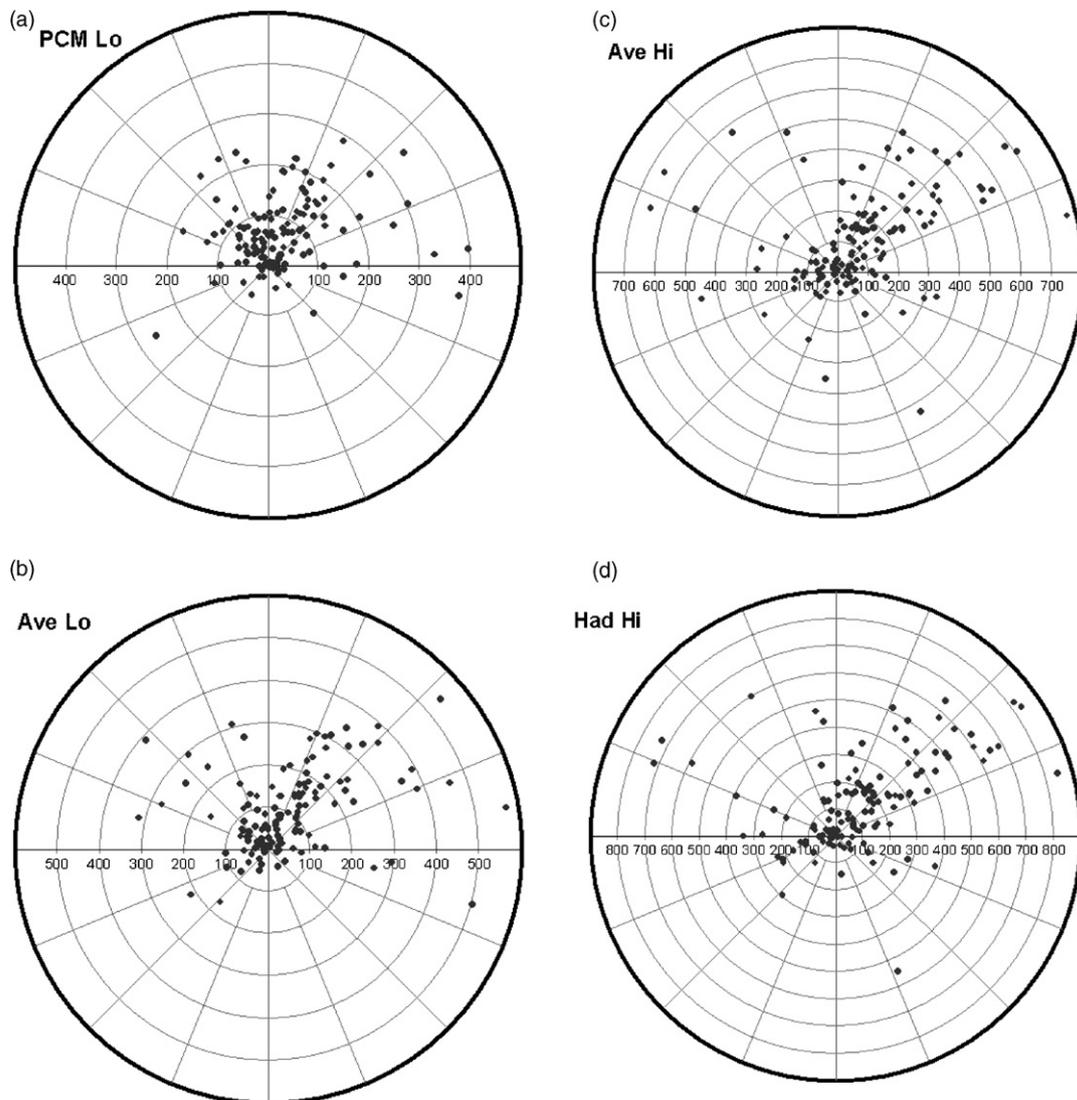


Fig. 2. Potential changes in distance and direction of mean centers of suitable habitat for 134 species, according to the (a) Parallel Climate Model – low emissions (PCM lo) (note the 0–500 km scale on the spokes); (b) average low emission scenarios (PCM, Hadley, GFDL, 0–600 km scale); (c) average high emission scenarios (PCM, Hadley, GFDL, 0–800 km); and (d) HadleyCM3 model – high emissions (Had hi) (0–900 km scale).

species such as *Betula papyrifera* (paper birch), *Populus tremuloides* (quaking aspen), *P. balsamifera* (balsam poplar), *A. balsamea* (balsam fir), *Thuja occidentalis* (northern white-cedar), *Acer nigrum* (black maple), *Picea rubens* (red spruce), *Picea glauca* (white spruce). Notice that many of these species are common components of the spruce-fir zone. Species showing increases of area-weighted importance values include *Quercus stellata* (post oak), *Q. marilandica* (blackjack oak), *Carya illinoensis* (pecan), *C. texana* (black hickory), *Gleditsia triacanthos* (honeylocust), and *Morus rubra* (red mulberry) (Supplement 3).

### 3.5. Changes in mean center of spatial data

The potential changes in mean centers of suitable habitat under various scenarios of climate change generally show movement in a northerly direction, with a longer distance of movement in the hotter (high emission) scenarios. For example, the map of sugar maple shows a general northward-moving set of ellipses of one standard deviation of the data (Fig. 1a). However, *Fagus grandifolia* (American beech) exemplifies a situation with the mean center moving south due to a general loss in abundance (not necessarily area) of suitable habitat in the currently rich zones of New England and New York (Fig. 1b). The mean center locations and potential movements in distance and direction are tabulated for each species and under four possible scenarios (Supplement 4). We also have maps like Fig. 1 for all species available online at <http://www.nrs.fs.fed.us/atlas>.

When we evaluate the mean center distances and directions of all species together across the entire eastern United States, we see some patterns and trends (Table 6, Fig. 2). The great majority of species move northward, and for these species, the high emission scenarios (Fig. 2c and d) push the habitat further north than the low emission scenarios (Table 6, Fig. 2a and b). For example, the Had hi scenario moved suitable habitat northward in excess of 400 km for 26 species (Table 6). Interestingly, the high emission scenarios also pushed several more species in a general southward direction. In most cases, the southward trend was due more to geographical or physiographic anomalies rather than biological or physiological aspects of the species under climate change. For example, a species may lose importance in the northern parts of its range but remain in the highlands of southern Appalachia, or a species may lose importance in northern Minnesota/Wisconsin/Michigan but retain habitat in southern New England. Even if the area of habitat remains the same into the future, the mean center would move south if the importance drops disproportionately more in the northern part of the species range. Most of the species of significance move north or northeast (Fig. 2).

### 3.6. Analysis of dominants, gainers, and losers by state

In this analysis, we identified the dominant species in the eastern U.S., selected regions (Fig. 3), and the states within the region. We then evaluated what our models suggest with respect to the potential change in suitable habitat for the top

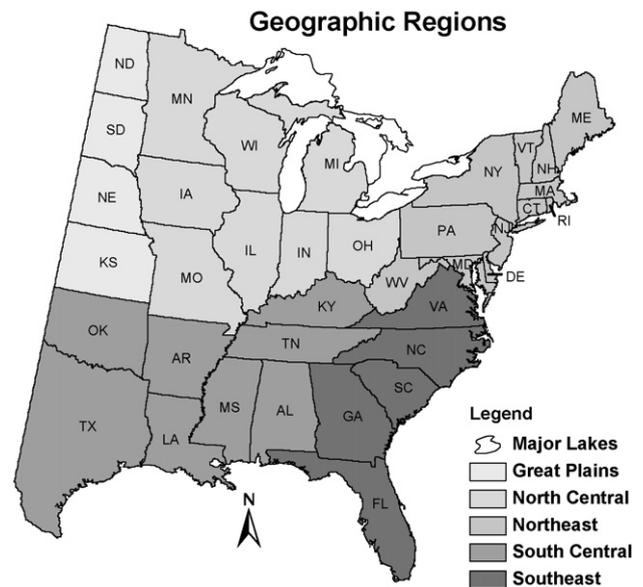


Fig. 3. Regions and states as defined for summarization in Table 7.

three current species according to the average low and high emission scenarios (Table 7). A total of 34 species are required to rank the top three for each state and region, including the eastern U.S. (Table 7). The species securing one of the top three positions most frequently are red maple (*Acer rubrum*, 24 out of 44 states/regions), sugar maple (*A. saccharum*, 12/44), and loblolly pine (*Pinus taeda*, 12/44). These are followed by *Ulmus americana* and *Liquidambar styraciflua* with 10/44 each. If tallied by genus, *Quercus* sp. appears in the top three category 22 times, while *Pinus* sp. appears 21 times (Table 7). Remember that these importance values are based equally on the number of stems and the basal area for each species, so that species with extremely large numbers of medium-sized stems will often emerge as more important than the larger canopy trees with fewer stems. For example, an oak appears only once as the top species but many states in the Central Hardwoods region have a mixture of oak species dominating the canopy, with many smaller *A. rubrum* stems in the midstory.

If we average the percentage values of current for the top ranked species in each state/region, we see an overall reduction to 82% of current area-weighted importance values under the Ave lo scenario and 65% under the Ave hi scenario (Table 7). The same pattern holds for the second ranked (83 and 73% of current importance) and third ranked (85 and 77% of current importance): the greater the emissions, the greater the loss of primary species importance. Although there are some species which seem to be enhanced in the changed climate (e.g., *P. taeda*, *U. americana*, *Acer saccharinum*, *Quercus macrocarpa*, and *Populus deltoides*), most species of high rank are diminished in suitable habitat under climate change.

### 3.7. Species-level maps

We prepared maps for each species based on FIA, current model, Had hi, Ave hi, Ave lo, and PCM lo that also reflect our

Table 7  
Top three species currently in each region and state, along with the percentages of current projected under average low and high emission scenarios

State/region	First species	Lo	Hi	Second species	Lo	Hi	Third species	Lo	Hi
Eastern US	<i>Acer rubrum</i>	76	62	<i>Pinus taeda</i>	118	123	<i>Ulmus americana</i>	115	114
Northeast	<i>Acer rubrum</i>	80	49	<i>Acer saccharum</i>	79	48	<i>Fraxinus americana</i>	83	57
North Central	<i>Ulmus americana</i>	113	93	<i>Populus tremuloides</i>	39	19	<i>Acer saccharum</i>	60	33
Great Plains	<i>Ulmus americana</i>	116	100	<i>Fraxinus pennsylvanica</i>	118	116	<i>Celtis occidentalis</i>	120	91
Southeast	<i>Pinus taeda</i>	111	108	<i>Acer rubrum</i>	66	63	<i>Pinus elliotii</i>	123	130
South Central	<i>Pinus taeda</i>	116	113	<i>Liquidambar styraciflua</i>	101	105	<i>Acer rubrum</i>	80	85
Alabama	<i>Pinus taeda</i>	105	96	<i>Liquidambar styraciflua</i>	89	91	<i>Quercus nigra</i>	105	96
Arkansas	<i>Pinus taeda</i>	126	113	<i>Liquidambar styraciflua</i>	113	111	<i>Quercus alba</i>	62	58
Connecticut	<i>Acer rubrum</i>	61	29	<i>Pinus strobus</i>	50	33	<i>Quercus rubra</i>	74	42
Delaware	<i>Acer rubrum</i>	63	50	<i>Liquidambar styraciflua</i>	127	117	<i>Quercus alba</i>	60	41
District fo Columbia	<i>Acer rubrum</i>	42	42	<i>Liriodendron tuliperfia</i>	15	15	<i>Quercus alba</i>	68	64
Florida	<i>Pinus elliotii</i>	105	104	<i>Taxodium distichum</i> (var. <i>nutans</i> )	98	110	<i>Quercus virginiana</i>	107	109
Georgia	<i>Pinus taeda</i>	101	95	<i>Liquidambar styraciflua</i>	89	88	<i>Pinus elliotii</i>	113	103
Illinois	<i>Ulmus americana</i>	133	54	<i>Quercus alba</i>	60	42	<i>Prunus serotina</i>	35	22
Indiana	<i>Acer saccharum</i>	30	10	<i>Ulmus americana</i>	89	42	<i>Fraxinus americana</i>	42	29
Iowa	<i>Ulmus americana</i>	142	104	<i>Quercus macrocarpa</i>	126	115	<i>Acer saccharinum</i>	136	113
Kansas	<i>Celtis occidentalis</i>	67	43	<i>Ulmus americana</i>	61	37	<i>Fraxinus pennsylvanica</i>	79	77
Kentucky	<i>Acer saccharum</i>	11	5	<i>Acer rubrum</i>	49	54	<i>Quercus alba</i>	97	86
Louisiana	<i>Pinus taeda</i>	94	83	<i>Liquidambar styraciflua</i>	85	90	<i>Quercus nigra</i>	87	86
Manie	<i>Abies balsamea</i>	29	16	<i>Acer rubrum</i>	116	91	<i>Picea rubens</i>	37	31
Maryland	<i>Acer rubrum</i>	56	42	<i>Quercus bicolor</i>	84	68	<i>Maclura pomifera</i>	36	27
Massachusetts	<i>Acer rubrum</i>	72	33	<i>Pinus strobus</i>	47	31	<i>Quercus rubra</i>	81	47
Michigan	<i>Acer rubrum</i>	80	62	<i>Acer saccharum</i>	55	33	<i>Populus tremuloides</i>	34	11
Minnesota	<i>Populus tremuloides</i>	42	19	<i>Quercus macrocarpa</i>	125	130	<i>Acer negundo</i>	114	151
Mississippi	<i>Pinus taeda</i>	102	95	<i>Liquidambar styraciflua</i>	90	92	<i>Quercus nigra</i>	112	104
Missouri	<i>Quercus alba</i>	53	44	<i>Quercus velutina</i>	85	69	<i>Ulmus americana</i>	64	43
Nebraska	<i>Populus deltoids</i>	119	113	<i>Fraxinus pennsylvanica</i>	153	145	<i>Juniperus virginiana</i>	114	89
New Hampshire	<i>Acer rubrum</i>	104	64	<i>Pinus strobus</i>	66	51	<i>Acer saccharum</i>	80	67
New Jersey	<i>Acer rubrum</i>	61	42	<i>Fraxinus americana</i>	45	30	<i>Pinus rigida</i>	86	85
New York	<i>Acer rubrum</i>	89	54	<i>Acer saccharum</i>	73	44	<i>Fraxinus americana</i>	84	46
North Carolina	<i>Pinus taeda</i>	129	119	<i>Acer rubrum</i>	52	44	<i>Liquidambar styraciflua</i>	103	101
North Dakota	<i>Acer negundo</i>	94	97	<i>Quercus macrocarpa</i>	93	132	<i>Ulmus americana</i>	110	194
Ohio	<i>Acer saccharum</i>	45	9	<i>Fraxinus americana</i>	41	22	<i>Ulmus americana</i>	81	34
Oklahoma	<i>Ulmus alata</i>	114	125	<i>Pinus echinata</i>	118	127	<i>Quercus marilandica</i>	123	111
Pennsylvania	<i>Acer rubrum</i>	66	31	<i>Prunus serotina</i>	46	19	<i>Acer saccharum</i>	79	37
Rhode Island	<i>Acer rubrum</i>	58	26	<i>Pinus strobus</i>	40	31	<i>Quercus rubra</i>	60	29
South Carolina	<i>Pinus taeda</i>	93	78	<i>Liquidambar styraciflua</i>	79	72	<i>Acer rubrum</i>	73	75
South Dakota	<i>Fraxinus pennsylvanica</i>	149	153	<i>Populus deltoides</i>	210	233	<i>Quercus macrocarpa</i>	113	162
Tennessee	<i>Acer rubrum</i>	66	61	<i>Quercus alba</i>	84	77	<i>Liriodendron tuliperfia</i>	39	34
Texas	<i>Pinus taeda</i>	90	72	<i>Liquidambar styraciflua</i>	82	77	<i>Ulmus alata</i>	106	117
Vermont	<i>Acer saccharum</i>	70	52	<i>Acer rubrum</i>	105	80	<i>Fagus grandifolia</i>	78	45
Virginia	<i>Acer rubrum</i>	54	40	<i>Liriodendron tuliperfia</i>	40	21	<i>Pinus taeda</i>	177	208
West Virginia	<i>Acer rubrum</i>	62	37	<i>Acer saccharum</i>	60	20	<i>Quercus prinus</i>	68	50
Wisconsin	<i>Populus tremuloides</i>	39	16	<i>Acer rubrum</i>	78	58	<i>Acer saccharum</i>	62	37

estimate of model reliability (Figs. 4–5). We have included in print two species: one of large economic value but subject to decrease (*Acer sacharum*, sugar maple, Fig. 4), and one southern pine species with potential to move northward and gain significant importance (*Pinus elliotii*, slash pine, Fig. 5). As supplemental material to this paper, we show three important northern (spruce-fir) species with modeled reduction in importance of suitable habitat: *Abies balsamea* (balsam fir, Supplement 5), *Picea mariana* (black spruce, Supplement 6), and *P. rubens* (red spruce, Supplement 7); one northern species modeled to lose importance: *Populus tremuloides* (quaking aspen, Supplement 8); a species of moderate reliability with new expansion of suitable habitat northward: *Quercus falcata falcata* (southern red oak, Supplement 9); and a rare species with new

habitat according to a model of low reliability: *Q. shumardii* (Shumard's oak, Supplement 10). As with other data and maps, they are all available online at <http://www.nrs.fs.fed.us/atlas>.

### 3.8. Forest-type maps

The forest-type maps resulting from the combination of species provides a perspective on how the suitable habitat might change at this biological level under various scenarios of climate change (Fig. 6). Most of the changes are apparent in the northern latitudes, especially the northeastern United States (Iverson et al., in press-b). We find that, in future, only PCM lo (the least harsh scenario) retains any presence of suitable habitat for the spruce-fir type in the United States. Habitat for

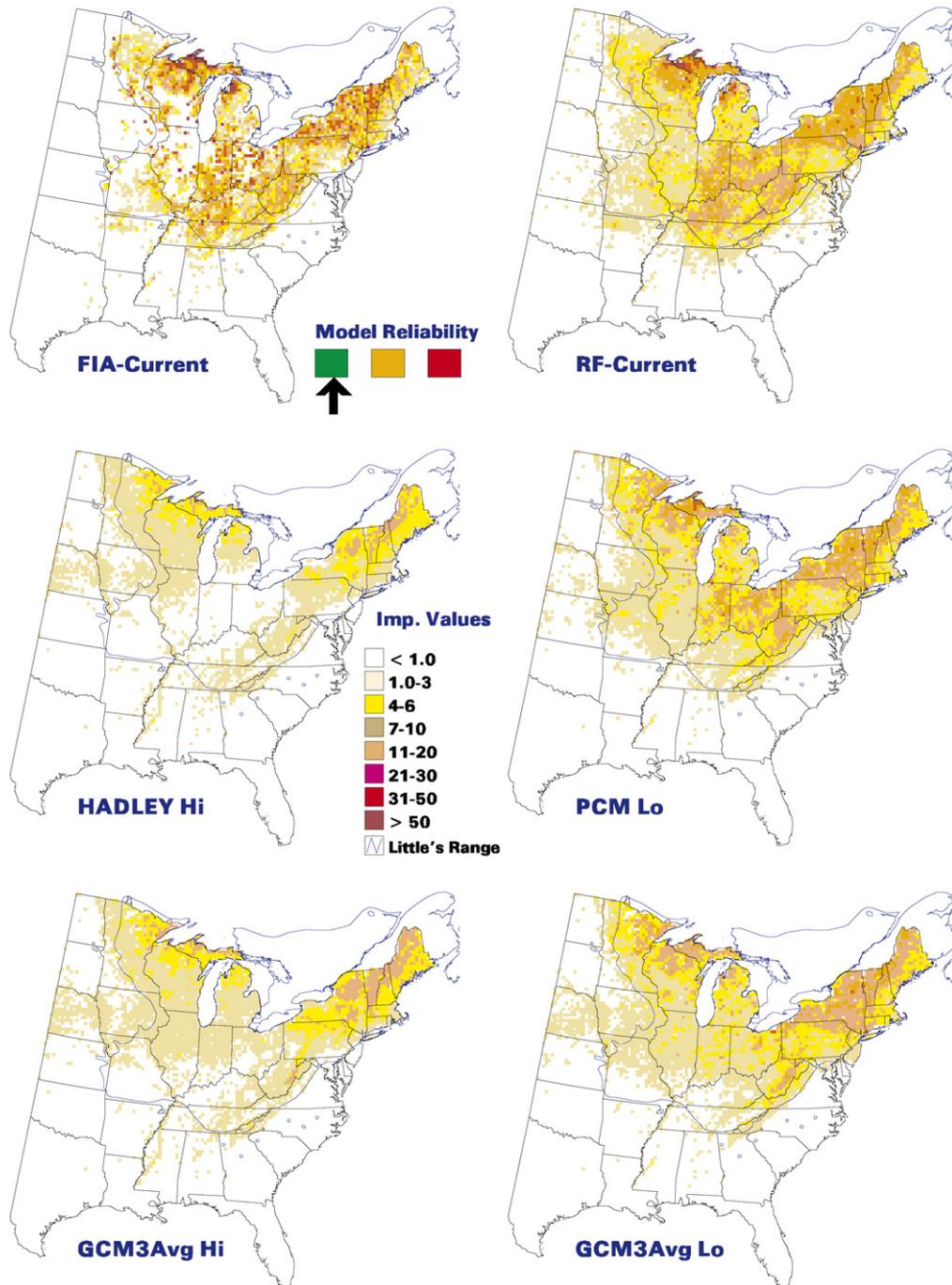
**sugar maple - *Acer saccharum* - (318)**

Fig. 4. Maps of current and potential future suitable habitat for *Acer saccharum* (sugar maple) including the FIA estimate of current distribution of abundance, the modeled current map, and scenarios of Parallel Climate Model – low emissions (PCM lo), average of three models – low emissions (Ave lo), average of three models – high emissions (Ave hi), and HadleyCM3 model – high emissions (Had hi).

the white-red-jack pine type is eliminated according to our model, though this type came out as sporadic to start with in our model algorithm, and thus more difficult to model future habitat. The aspen-birch type is severely curtailed in suitable habitat under low emissions, but is eliminated under higher emissions. The oak-hickory type is modeled to expand into the north, especially under higher emission scenarios. Though the maple-beech-birch is fairly stable under low emissions, its

habitat is reduced under higher emissions as oak-hickory and oak-pine expand. In this analysis, the southern pine types remain fairly stable even though individual southern pine habitat increases to the north for many pines. The explanation for this pattern is that the oak species also generally increase so that the proportions stay similar, or even favor oak-pine over loblolly pine for a portion of the current southern pine habitat (Fig. 6).

### slash pine - *Pinus elliottii* - (111)

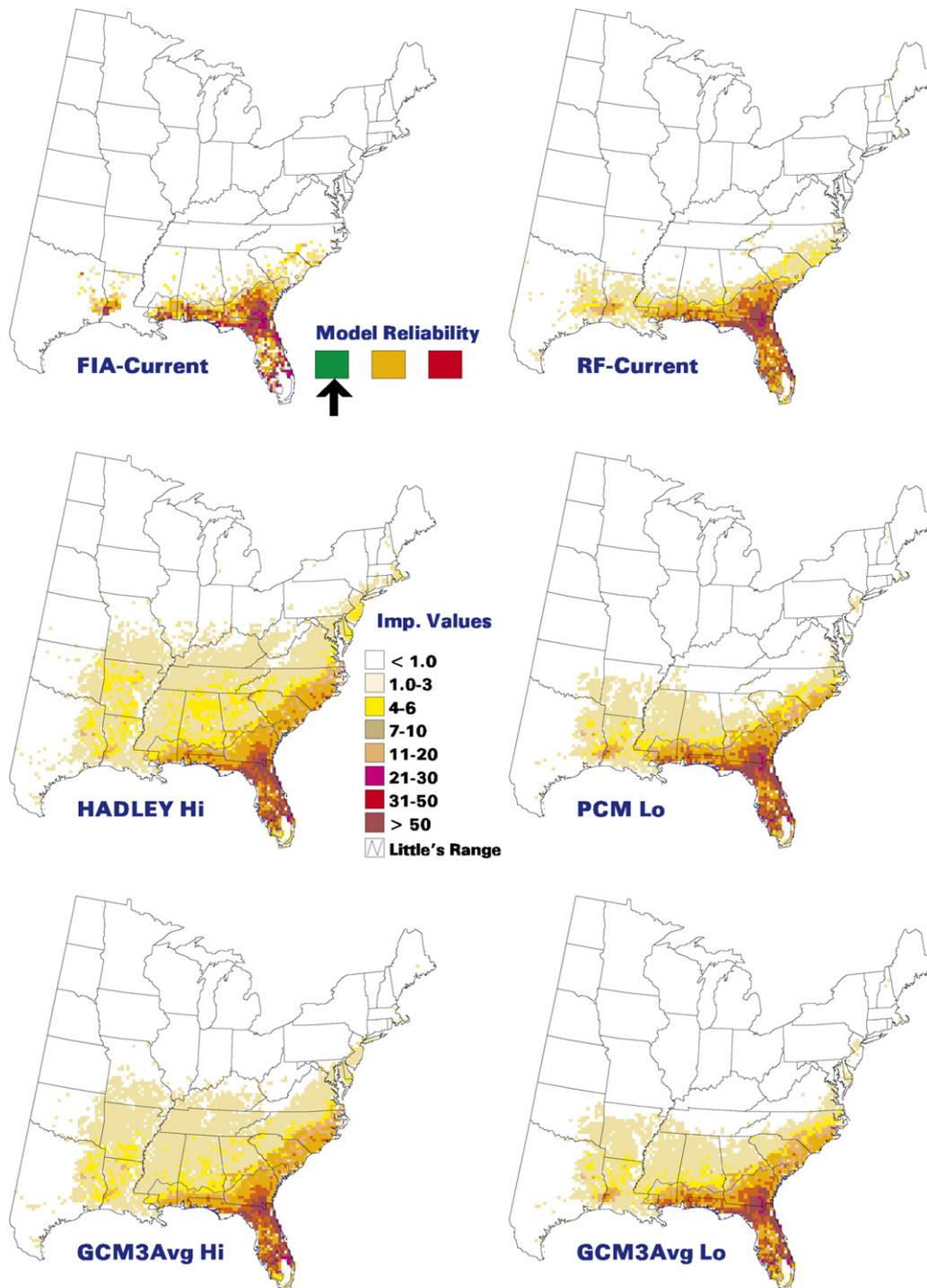


Fig. 5. Maps of current and potential future suitable habitat for *Pinus elliottii* (slash pine) including the FIA estimate of current distribution of abundance, the modeled current map, and scenarios of PCM Parallel Climate Model – low emissions (PCM lo), average of three models – low emissions (Ave lo), average of three models – high emissions (Ave hi), and HadleyCM3 model – high emissions (Had hi).

#### 4. Discussion

The forests of the eastern United States are likely to undergo radical changes as the climate changes. Evidence that shifts are already taking place continue to mount (e.g., Soja et al., 2007), and in ways predicted in this modeling effort. Similar work in

the western United States (Rehfeldt et al., 2006) has also shown modeled changes to be in line with shifts reported by Soja et al. (2007). Although we cannot put an exact timeline to the potential changes outlined here, we estimate suitable habitat will increase for many species, especially the southern species with expansion northward. Using the more dependable metric

### Forest Type Maps

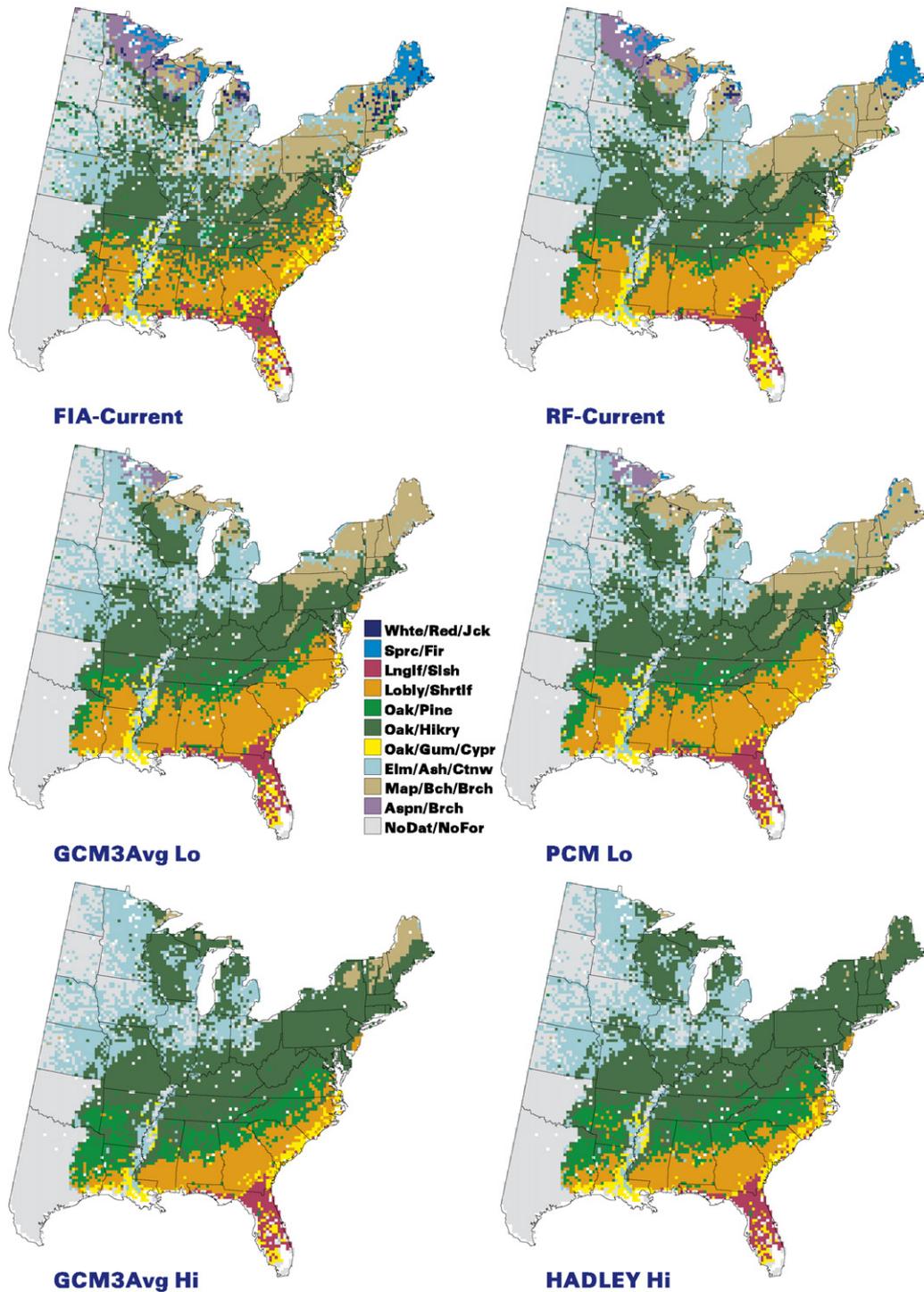


Fig. 6. Maps of current and potential future suitable habitat for the USDA Forest Service forest types, including the FIA estimate of current distribution of abundance, the modeled current map, and scenarios of Parallel Climate Model – low emissions (PCM lo), average of three models – low emissions (Ave lo), average of three models – high emissions (Ave hi), and HadleyCM3 model – high emissions (Had hi).

of area-weighted importance value, about 66 (61–68 depending on emission scenario) of 134 species show the potential for increases of at least 10%, and 8 (low emission) to 37 (high emission) species could increase in importance by at least 50%. Several of these species are currently important commercial species of oak (*Quercus*) or pine (*Pinus*). Increased habitat for

oak could indicate an increased commercial and wildlife resource (especially in the northern part of the country), but oaks currently are undergoing a regeneration crisis in the absence of fire or other agents that can partially open the canopy (Loftis and McGee, 1993; Iverson et al., 2004b). It is possible that some disturbances promoted by climate change may open

the canopy sufficiently to enhance the probability of oak regeneration. Additional research on this topic is needed. Besides the oaks and pines, many of the other expansion species are fairly small-ranged species that do not have a highly reliable model.

Another 54 species (50–58) show a loss of at least 10% in area-weighted importance value, and 14 (low emission) to 26 (high emission) species could drop by more than 50% in importance. There are many northern species that bound Canada in this 50% loss category, at least under the high emission scenarios: *Picea mariana*, *Acer spicatum*, *Betula papyrifera*, *Abies balsamea*, *Populus tremuloides*, *Populus grandidentata*, *Acer nigrum*, *Betula alleghaniensis*, *Picea rubens*, *Acer pensylvanicum*, and *Acer saccharum*. The evaluation of forest types reveal essentially the same thing: the models suggest a retreat of the spruce-fir zone as seen in the past (DeHayes et al., 2000). Additionally, the forest-type summaries show loss of the aspen-birch, white-red-jack pine, and maple-beech-birch habitat, as well as gains in oak-hickory and oak-pine. The extent of the changes depends largely on the emission scenario selected by humans over the next century – changes would be much less dramatic if humans follow a low emissions pathway. The species listed as potential losers currently provide much of the commercial and tourism value of the North. The potential economic impact of such changes could be substantial.

Coupled with the changing habitat for these species is the increasing onslaught of disturbances inclined to accelerate compositional changes: pests, diseases, land-use change, invasives, fire, and climatic disturbances. Pests such as the Hemlock woolly adelgid (Paradis et al., in press) and emerald ash borer (Poland and McCullough, 2006; Iverson et al., in press-a), spruce budworm, and pine bark beetle, and diseases such as the white pine blister rust, beech bark disease, maple decline, and spruce/fir decline (cited in Ayers and Lombardero, 2000) are threatening and killing several of the species likely to substantially change under climate change. Thus, the compositional changes of forests will be accelerated by these disturbances. Invasive plants also are likely to spread under climate change as niches open, because the invasives are adapted to wider conditions and rapid colonization and growth after disturbance and elevated carbon dioxide (Williamson, 1999; Weltzin et al., 2003). Of course, other human-derived disturbances associated with changes in land use and land cover have had and will continue to have profound impacts on the species composition (Foster and Aber, 2004).

A changing climate has already been shown to be increasing other disturbances, with more changes coming (Hayhoe et al., 2006). Climatic effects such as increases in wind and ice damage, hurricane intensity, heavy precipitation events, drought in the later parts of the growing season, flooding during the growing season, and warmer winter and summer temperatures (Hayhoe et al., 2006) can increase stress on species, leading to further changes. An analysis of 806 northern temperate trees and shrubs (worldwide) showed that few species can tolerate more than one of the following stresses: shade, drought, or waterlogging (Niinemets and Valladares,

2006). Climate change will change the proportions of these stresses, e.g. increases in both drought and waterlogging potential, again leading to changes in species composition. Wildfire is also likely to increase under climate change, at least in some portions of the country (McKenzie et al., 2004; Keane et al., 2004). In places like the uninterrupted forests in Maine, the New Jersey pine barrens, and the pine forests of the Southeast, fire could have an especially substantial effect on hastening species changes that are undergoing changes in habitat suitability.

With respect to the evaluation of mean centers of current and potential future habitat, the habitat for most species generally moves northeast. As expected, with each hotter scenario, the distances increase for movement of mean center of habitat. The maximum distances of habitat centers range from about 400 km with PCM lo to about 800 km with Had hi scenarios. The high-emission trajectory shows a much higher maximum movement and a much larger number of species moving compared to the low-emission trajectory.

Importantly, we do not here model potential species ranges by the year 2100. We model the suitable habitat related to each species. This suitable habitat is primarily based on climate, though soil, elevation, and land-use variables also are also important for many species. Notably, we have not modeled the changes in soil or land-use that would also likely change under climate change. For example, agricultural practices or carbon/nutrient retention in soils would likely change. Because of the long-lived nature of trees, we would not expect the changes presented here to be realized by 2100 unless disturbance agents exert a profound acceleration effect on the changes. We also would expect that there is a greater likelihood that disturbance agents would hasten declines to a greater degree than they would accelerate emergence of new species entering newly available suitable habitat; however, if the species already is present (like some of the common pines), they may increase in importance as the competitors decrease. We have attempted to determine actual estimated ranges for several species in other work using a companion model (SHIFT). We found that the lag times and fragmented nature of the remaining forests greatly slow migration rates. We estimated that, for four species, less than 15% of the suitable habitat would have a 1 in 50 chance of being naturally colonized within 100 years (Iverson et al., 2004c,d). Thus, it appears that humans could play a vital role, either accidentally or purposefully, in moving selected species into their newly emerging suitable habitat, and in modulating the role of competition through vegetation management practices.

## 5. Conclusions

We model and map the potential changes in degrees of suitable habitat for 134 individual tree species in the eastern United States under three recent GCM models and two emission scenarios. We also use a tri-model approach to assess the reliability of each model. These models show potentially very large changes in species importance and forest type habitat, especially under the higher emissions trajectory. Our

results show that species will have a lot less pressure to move, and species disruption will be much less severe, if we follow a path of lower emissions of greenhouse gases. Readers are encouraged to visit the companion website to obtain details on their favorite species or location: <http://www.nrs.fs.fed.us/atlas>.

## Acknowledgements

Thanks to the Northern Global Change Program, U.S. Forest Service, for support over several years, and to the Forest Inventory and Analysis units of the U.S. Forest Service, for forest data. The authors thank Katharine Hayhoe for providing the climate-scenario data. Special thanks to Hong He, Richard Birdsey, John Stanovick, Robert Keane, Susan Wright, and several unidentified reviewers for their helpful suggestions.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2007.07.023.

## References

- Ayers, M.P., Lombardero, M.J., 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* 262, 263–286.
- Breiman, L., 1996. Bagging predictors. *Mach. Learn.* 24, 123–140.
- Breiman, L., 2001. Random forests. *Mach. Learn.* 45, 5–32.
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 1984. *Classification and Regression Trees*. Wadsworth and Brooks/Cole, Monterey, CA.
- Cary, G.J., Keane, R.E., Gardner, R.H., Lavorel, S., Flannigan, M.D., Davies, I.D., Li, C., Lenihan, J.M., Rupp, T.S., Mouillot, F., 2006. Comparison of the sensitivity of landscape-fire-succession models to variation in terrain, fuel pattern, climate and weather. *Landscape Ecol.* 21, 121–137.
- Chaing, J., Iverson, L.R., Prasad, A.M., Brown, K., 2006. Interactions of changing climate and shifts in forest composition on stand carbon balance. In: *Ecological Society of America, 91st Annual Meetings*, Memphis, TN.
- Cotton, P.A., 2003. Avian migration phenology and global climate change. *Proc. Natl. Acad. Sci. U.S.A.* 100 (21), 12219–12222.
- Cushman, S.A., McKenzie, D., Peterson, D.L., Littell, J., McKelvey, K.S., 2007. Research agenda for integrated landscape modeling. General Technical Report RMRS-GTR-194. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
- Davis, M.B., Zabinski, C., 1992. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. In: Peters, R.L., Lovejoy, T.E. (Eds.), *Global Warming and Biological Diversity*. Yale University Press, New Haven, CT, pp. 297–308.
- DeHayes, D.H., Jacobson, G.L., Schaber, P.G., Bongarten, B., Iverson, L.R., Dieffenbacher-Krall, A., 2000. Forest responses to changing climate: lessons from the past and uncertainty for the future. In: Mickler, R.A., Birdsey, R.A., Hom, J.L. (Eds.), *Responses of Northern Forests to Environmental Change*. Springer-Verlag, New York, NY, (ecological studies series), pp. 495–540.
- Delworth, T.L., Broccoli, A.J., Rosati, A., Stouffer, R.J., et al., 2006. GFDL's CM2 global coupled climate models. Part 1. Formulation and simulation characteristics. *J. Climate* 19, 643–674.
- Fitter, A.H., Fitter, R.S.R., 2002. Rapid changes in flower time of British flowering plants. *Science* 296, 1689–1691.
- Foster, D., Aber, J., 2004. *Forests in Time*. Yale University Press, Cambridge, MA.
- Guisan, A., Theurillat, J.P., 2000. Equilibrium modelling of alpine plant distribution and climate change: how far can we go? *Phytocoenologia* 30, 353–384.
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009.
- Hagen-Zanker, A., Engelen, G., Hurkens, J., Vanhout, R., Uljee, I., 2006. *Map Comparison Kit 3. User Manual*, Research Institute for Knowledge Systems, Maastricht, The Netherlands.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R., Bartlein, P.J., 2001. Global change in forests: responses of species, communities, and biomes. *BioScience* 51 (9), 765–779.
- Hayhoe, K., Wake, C.P., Huntington, T.G., Luo, L., Schwartz, M.D., Sheffield, J., Wood, E.F., Anderson, B., Bradbury, J., DeGaetano, A., Troy, T., Wolfe, D., 2006. Past and future changes in climate and hydrological indicators in the U.S. Northeast. *Climate Dyn.* 28, 381–407.
- Ibanez, I., Clark, J.S., Dietze, M.C., Felley, K., Hersh, M., LaDeau, S., McBride, A., Welch, N.E., Wolosin, M.S., 2006. Predicting biodiversity change: outside the climate envelope, beyond the species–area curve. *Ecology* 87, 1896–1906.
- Iverson, L.R., Prasad, A.M., 1998. Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monogr.* 68, 465–485.
- Iverson, L.R., Prasad, A.M., Hale, B.J., Sutherland, E.K., 1999a. An atlas of current and potential future distributions of common trees of the eastern United States. General Technical Report NE-265, Northeastern Research Station, USDA Forest Service, Radnor, PA.
- Iverson, L.R., Prasad, A.M., Schwartz, M.W., 1999b. Modeling potential future individual tree-species distributions in the Eastern United States under a climate change scenario a case study with *Pinus virginiana*. *Ecol. Modell.* 115, 77–93.
- Iverson, L.R., Prasad, A.M., Liaw, A., 2004a. New machine learning tools for predictive vegetation mapping after climate change: Bagging and Random Forest perform better than regression tree analysis. In: Smithers, R. (Ed.), *Proceedings, UK-International Association for Landscape Ecology*, Cirencester, UK, pp. 317–320.
- Iverson, L.R., Prasad, A.M., Hutchinson, T.F., Rebeck, J., Yaussy, D., 2004b. Fire and thinning in an Ohio oak forest: grid-point analysis of fire behavior, environmental conditions, and tree regeneration across a topographic moisture gradient. In: Spetich, M. (Ed.), *Proceedings, Upland Oak Symposium*. Southern Research Station, USDA Forest Service, Starkville, MS.
- Iverson, L.R., Schwartz, M.W., Prasad, A.M., 2004c. Potential colonization of newly available tree species habitat under climate change: an analysis for five eastern US species. *Landscape Ecol.* 19, 787–799.
- Iverson, L.R., Schwartz, M.W., Prasad, A.M., 2004d. How fast and far might tree species migrate under climate change in the eastern United States? *Global Ecol. Biogeogr.* 13, 209–219.
- Iverson, L.R., Prasad, A., Bossenbroek, J., Sydnor, D., Schwartz, M.W. Modeling potential movements of an ash threat: the emerald ash borer. In: Pye, J., Raucher, M. (Eds.), *Advances in Threat Assessment and their Application to Forest and Rangeland Management*, in press-a. <http://www.threats.forestencyclopedia.net>.
- Iverson, L.R., Prasad, A.M., Matthews, S., in press. Modelling potential climate change impacts on the trees of the Northeastern United States. *Mitigat. Adapt. Strateg.*, in press-b.
- Joyce, L.A., Birdsey, R. (Technical eds.), 2000. The impact of climate change on America's forests: a technical document supporting the 2000 USDA Forest Service RPA Assessment. General Technical Report 59. Rocky Mountain Research Station, USDA Forest Service, Fort Collins, CO.
- Keane, R.E., Cary, G.J., Davies, I.D., Flannigan, M.D., Gardner, R.H., Lavorel, S., Lenihan, J.M., Li, C., Rupp, S.T., 2004. A classification of landscape fire succession models: spatial simulations of fire and vegetation dynamics. *Ecol. Modell.* 179, 3–27.
- Kirschbaum, M.U.F., 2000. Forest growth and species distribution in a changing climate. *Tree Physiol.* 20, 309–322.
- Laliberte, A.S., Ripple, W.J., 2004. Range contractions of North American carnivores and ungulates. *BioScience* 54 (2), 123–138.
- Little, E.L., 1971. *Atlas of United States trees. Conifers and important hardwoods*. Miscellaneous Publication 1146, vol.1. U.S. Department of Agriculture, Forest Service, Washington, DC.

- Little, E.L., 1977. Atlas of United States Trees. Minor Eastern Hardwoods. Miscellaneous Publication 1342, vol.4. U.S. Department of Agriculture, Forest Service, Washington, DC.
- Loftis, D.L., McGee, C.E. (Eds.), 1993. Oak regeneration: serious problems, practical recommendations. General Technical Report SE-84, Southeastern Forest Experiment Station, Asheville, NC.
- Lovejoy, T.E., Hannah, L., 2005. Climate Change and Biodiversity. Yale University Press, New Haven, CT.
- McKenney, D.E.W., Hutchinson, M.F., Kesteven, J.L., Venier, L.A., 2001. Canada's plant hardiness zones revisited using modern climate interpolation techniques. *Can. J. Plant Sci.* 47, 351–357.
- McKenzie, D., Gedolof, Z.E., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. *Conserv. Biol.* 18 (4), 890–902.
- Melillo, J.M., Callaghan, T.V., Woodward, F.I., Salati, E., Sinha, S.K., 1990. Effects on ecosystems. In: Houghton, J.T., Jenkins, G.J., Ephraums, J.J. (Eds.), *Climate Change: the IPCC Scientific Assessment*. Cambridge University Press, Cambridge, UK, pp. 283–310.
- Miles, P.D., Brand, G.J., Alerich, C.L., Bednar, L.R., Woudenberg, S.W., Glover, J.F., Ezzell, E.N., 2001. The forest inventory and analysis database: database description and users manual version 1.0. General Technical Report NC-218, North Central Research Station, USDA Forest Service, St. Paul, MN.
- Nakicenovic, N., et al., 2000. IPCC special report on emissions scenarios. Cambridge University Press, Cambridge, UK.
- National Assessment Synthesis Team, 2001. Climate change impacts on the United States: the potential consequences of climate variability and change. Foundation report. Cambridge University Press, Cambridge, UK.
- Niinemets, U., Valladares, F., 2006. Tolerance to shade, drought, and water-logging of temperate Northern Hemisphere trees and shrubs. *Ecol. Monogr.* 76, 521–547.
- Olson, R.J., Emerson, C.J., Nungesser, M.K., 1980. Geocology: a county-level environmental data base for the coterminous United States, Publication 1537. Oak Ridge National Laboratory Environmental Sciences, Oak Ridge, TN.
- Paradis, A., Elkinton, J., Hayhoe, K. Effect of winter temperatures on the survival of hemlock woolly adelgid, *Adelges tsugae*, and the potential impact of global warming on its future range in North America. *Mitigat. Adapt. Strateg. Global Change*, in press.
- Parmesan, C., Galbraith, H., 2004. Observed impacts of climate change in the United States. *Pew Center on Global Climate Change*, Arlington, VA.
- Poland, T., McCullough, D.G., 2006. Emerald ash borer: invasion of the urban forest and the threat to North America's ash resource. *J. Forestry* 104 (April/May), 118–124.
- Pope, V.D., 2000. The impact of new physical parameterizations in the Hadley Centre climate model – HadCM3. *Climate Dyn.* 16, 123–146.
- Prasad, A.M., Iverson, L.R., 1999. A Climate Change Atlas for 80 Forest Tree Species of the Eastern United States [database]. <http://www.fs.fed.us/ne/delaware/atlas>.
- Prasad, A.M., Iverson, L.R., Liaw, A., 2006. Newer classification and regression tree techniques: Bagging and Random Forests for ecological prediction. *Ecosystems* 9, 181–199.
- Rehfeldt, G.E., Crookston, N.L., Warwell, M.V., Evans, J.S., 2006. Empirical analysis of plant–climate relationships for the western United States. *Int. J. Plant Sci.* 167, 1123–1150.
- Retuerto, R., Carballeira, A., 2004. Estimating plant responses to climate by direct gradient analysis and geographic distribution analysis. *Plant Ecol.* 170 (2), 185–202.
- Riitters, K.H., Wickham, J.D., O'Neill, R.V., Jones, K.B., Smith, E.R., Coulston, J.W., Wade, T.G., Smith, J.H., 2002. Fragmentation of continental United States forests. *Ecosystems* 5, 815–822.
- Scheller, R.M., Mladenoff, D.J., 2007. Forest landscape simulation models: tools and strategies for understanding large-scale forested ecosystems. *Landscape Ecol.* 22, 491–505.
- Scheller, R.M., Domingo, J.B., Sturtevant, B.R., Williams, J.S., Rudy, A., Gustafson, E.J., Mladenoff, D.J., 2007. Design, development, and application of LANDIS-II, a spatial landscape simulation model with flexible spatial and temporal resolution. *Ecol. Modell.* 201, 409–419.
- Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N., O'Connor, R.J., 2006. Predicting extinctions as a result of climate change. *Ecology* 87 (7), 1611–1615.
- Soil Conservation Service, 1991. State soil geographic data base (STATSGO) data users guide, Miscellaneous Publication 1492. U.S. Department of Agriculture, Soil Conservation Service, Washington, DC.
- Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukinin, A.I., Parfenova, E.E., Chapin, F.S., Sackhouse, P.W., 2007. Climate-induced boreal forest change: predictions versus current observations. *Global Planet. Change* 56, 274–296.
- Therneau, T.M., Atkinson, E.J., 1997. An introduction to recursive partitioning using the RPART routines. Technical Report #61, Mayo Clinic, Rochester, MN.
- Thuiller, W., Lavorel, S., Sykes, M.T., Araujo, M.B., 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Divers. Distrib.* 12, 49–60.
- U.S. Geological Survey, 1990. Digital elevation models: U.S. Geological Survey Data User's Guide 5. U.S. Geological Survey, Reston, VA.
- Washington, W.M., Weatherly, J.W., Meehl, G.A., Semtner Jr., A.J., Bettge, T.W., Craig, A.P., Strand Jr., W.G., Arblaster, J.M., Wayland, V.B., James, R., Zhang, Y., 2000. Parallel climate model (PCM) control and transient simulations. *Climate Dyn.* 16, 755–774.
- Webb III, T., Bartlein, P.J., 1992. Global changes during the last 3 million years: climatic controls and biotic responses. *Annu. Rev. Ecol. Syst.* 23, 141–173.
- Weltzin, J.F., Belote, R.T., Sanders, J.J., 2003. Biological invaders in a greenhouse world: will elevated CO<sub>2</sub> fuel plant invasions? *Front. Ecol. Environ.* 1, 146–153.
- Williamson, M., 1999. Invasions. *Ecography* 22, 5–12.
- Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B., Kunin, W.E., 2004. Spatial patterns in species distributions reveal biodiversity change. *Nature* 432, 393–396.
- Wood, A.W., Maurer, E.P., Kumar, A., Lettenmaier, D.P., 2002. Long-range experimental hydrologic forecasting for the eastern United States. *J. Geophys. Res.* 107 Article No.4429.
- Yates, D.N., Kittel, T.G.F., Cannon, R.F., 2000. Comparing the correlative Holdridge model to mechanistic biogeographical models for assessing vegetation distribution response to climatic change. *Climatic Change* 44, 59–87.