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PREDICTING ABUNDANCE OF 80 TREE SPECIES FOLLOWING CLIMATE CHANGE IN THE EASTERN UNITED STATES

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Abstract. Projected climate warming will potentially have profound effects on the earth's biota, including a large redistribution of tree species. We developed models to evaluate potential shifts for 80 individual tree species in the eastern United States. First, environmental factors associated with current ranges of tree species were assessed using geographic information systems (GIS) in conjunction with regression tree analysis (RTA). The method was then extended to better understand the potential of species to survive and/or migrate under a changed climate. We collected, summarized, and analyzed data for climate, soils, land use, elevation, and species assemblages for >2100 counties east of the 100th meridian. Forest Inventory Analysis (FIA) data for >100 000 forested plots in the East provided the tree species range and abundance information for the trees. RTA was used to devise prediction rules from current species–environment relationships, which were then used to replicate the current distribution as well as predict the future potential distributions under two scenarios of climate change with twofold increases in the level of atmospheric CO_2. Validation measures prove the utility of the RTA modeling approach for mapping current tree importance values across large areas, leading to increased confidence in the predictions of potential future species distributions.

With our analysis of potential effects, we show that roughly 30 species could expand their range and/or weighted importance at least 10%, while an additional 30 species could decrease by at least 10%, following equilibrium after a changed climate. Depending on the global change scenario used, 4–9 species would potentially move out of the United States to the north. Nearly half of the species assessed (36 out of 80) showed the potential for the ecological optima to shift at least 100 km to the north, including seven that could move >250 km. Given these potential future distributions, actual species redistributions will be controlled by migration rates possible through fragmented landscapes.

Key words: climate change; envelope analysis; forest inventory; geographic information systems (GIS); global change; landscape ecology; predictive vegetation mapping; regression tree analysis (RTA); species–environment relationships; tree species distribution; tree species migration; tree species ranges.

INTRODUCTION

The buildup of anthropogenic greenhouse gases is related to a general warming trend on the planet, and current estimates from global circulation models (GCMs) predict 1°–4.5°C temperature increases as a result of doubling atmospheric CO_2, probably by the end of the next century (Kattenberg et al. 1996). This trend suggests a potential to trigger major changes in the earth's living systems, including temperate forests. Many research lines, including this one, are devoted to predicting these potential major changes in the earth's biota, especially with respect to the potential necessary migration of plant species.

Studies of the Holocene, when there was climatic warming at a lower rate than is projected by current GCMs, show the following points with respect to species migration (Jacobson et al. 1987, Delcourt and Delcourt 1988, Davis and Zabinski 1992, Webb and Bartlein 1992, Malanson 1993): (1) Species did shift their geographical ranges, generally northward. (2) Species' responses were individualistic—the rates and direction of migration differed among taxa and species assemblages did not remain the same. (3) Species responded to climate change in an equilibrium manner, and, at the continental scale of evaluation, competition and dispersal mechanisms did not seem to play a large role in the responses of species. Migrations were occurring over thousands of years and over a relatively uninterrupted landscape. Under current greenhouse warming scenarios, however, the climate is projected to change at a faster rate. In today's fragmented landscapes, competition, dispersal ability, and nonequilibrium responses may be critical in the final species assemblage, and individual-species models are necessary to account for the expected individualistic responses.

With advances in the use of geographic information systems (GIS) and the increased abundance of data available for landscapes, several techniques can now

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be used to predict the geographic distribution of vegetation from mapped environmental variables (Franklin 1995). For continuous data, these include regression models, general linear models, general additive models, and regression tree models. Especially important drivers to vegetation models are climatic, edaphic, and topographic variables. At local scales, modeling of vegetation pattern depends largely on local variations of topography and geomorphology (e.g., Reed et al. 1993, Ertsen et al. 1995, Iverson et al. 1996*b*, 1997). At regional scales, overall vegetation patterns have been assumed to depend more on general climatic patterns (e.g., Booth 1990, Prentice et al. 1992, Woodward 1992, Box et al. 1993, Neilson 1995). To some extent, we evaluate both in this study.

Various GCMs are being built to simulate the future climate system, which can then be used to predict possible changes in the earth's forest biota. Several approaches are being taken at a number of scales and locations. Because such models cannot be truly validated (Rastetter 1996), multiple avenues of research are encouraged, with the hope of eventual convergence. Much discussion centers on the various approaches and the comparisons among them (e.g., McGuire et al. 1993, Hobbs 1994, Melillo et al. 1995). Several models assess changes in global biomes (e.g., Prentice et al. 1992, Woodward 1992, Neilson and Marks 1994), including recent models that couple vegetation effects directly into the GCMs so that feedbacks are continuously incorporated into the outcome (e.g., Foley et al. 1996), while others assess a selected number of species over a regional scale (e.g., Bonan and Sirois 1992, Mackey and Sims 1993, Burton and Cumming 1995, Dyer 1995, Hughes et al. 1996, Starfield and Chapin 1996). For example, Huntley et al. (1995) used a three-way climate response surface to model the present and future distributions of eight species in Europe.

However, there have been few or no studies that model the entire suite of major tree species, individually, across their continental ranges. Such an approach is the only way to begin to identify the possible new outcomes in species assemblages after climate change. Most of the previously cited studies also deal only with range shifts, not with projected shifts in the importance of species. In this study, we empirically model each of 80 species across the eastern United States, so that the different habitat requirements among species are accommodated by the models. We statistically evaluate, using regression tree analysis (RTA), the relationship of 33 environmental variables to tree importance values in the eastern United States, and then use the derived relationships to predict their present and potential future ranges and importance values. Our approach is unique in the sense that it is a multiple-species effort at a continental scale.

METHODS

Database generation

Data were extracted from several sources for land east of the 100th meridian (Fig. 1). The county was chosen as the mapping unit because it is the reporting unit for many sources of data and, for the most part except for some northern counties, has roughly the same area across the study region. The Modifiable Area Unit Problem, where spatial aggregations can lead to problems with scaling and zoning (Jelinski and Wu 1996), was an issue, though it was minimized by using percentages and area-weighted averages as input variables. We evaluated >100 environmental/land use/socioeconomic variables for each of nearly 2500 counties in the East. Because of missing tree information on some counties, only 2124 counties were finally mapped. To reduce autocorrelation and enable better interpretation, the final number of variables was reduced to 33 (Table 1) by (a) removing highly redundant variables as deduced via correlation analysis; (b) dropping variables selected by experts as excessively difficult to interpret; and (c) scoring 65 variables for their value in an earlier RTA run on all species and dropping the variables of lower importance. To evaluate overall importance of each of the resulting 33 variables, they were scored for frequency of occurrence and rank-based weight in the RTA outputs for the 80 species (Table 1).

Tree ranges and importance values.—The USDA Forest Service periodically determines the extent, condition, and volume of timber, growth, and removals of the Nation's forest land by the work of six Forest Service Forest Inventory and Analysis (FIA) units. Four FIA units produced a database of standard format called the Eastwide Data Base (EWDB) for the 37 states from North Dakota to Texas and east. These data are stored in three record types (Hansen et al. 1992): county data, plot data, and tree data. Plot locations are not precisely located but county location was provided for each plot. We used the data from >100 000 plots and nearly 3×10^6 trees to summarize the desired county-level information needed for this study. We evaluated 196 species of trees from the EWDB, but as described later, only 80 species were modeled due to sample restrictions.

We first summarized the information for individual forested plots. Tree records represented observations of seedlings, saplings, and overstory trees. Tree species, tree status, and diameter at breast height were combined with information on plot size to compute a single summary record for each plot. This record contained, by species, estimates of the average number of stems and total basal area of understory and overstory trees per unit area. From this information, we generated importance values (IV) for each species as follows:

$$\mathrm{IV}(x) = \frac{100\mathrm{BA}(x)}{\mathrm{BA(all\ species)}} + \frac{100\mathrm{NS}(x)}{\mathrm{NS(all\ species)}}$$

where x is a particular species on a plot, BA is basal area, and NS is number of stems (summed for overstory and understory trees). In monotypic stands, the IV would reach the maximum of 200. The IVs were rounded to decimal numbers with one exception. If $1 > \mathrm{IV}$

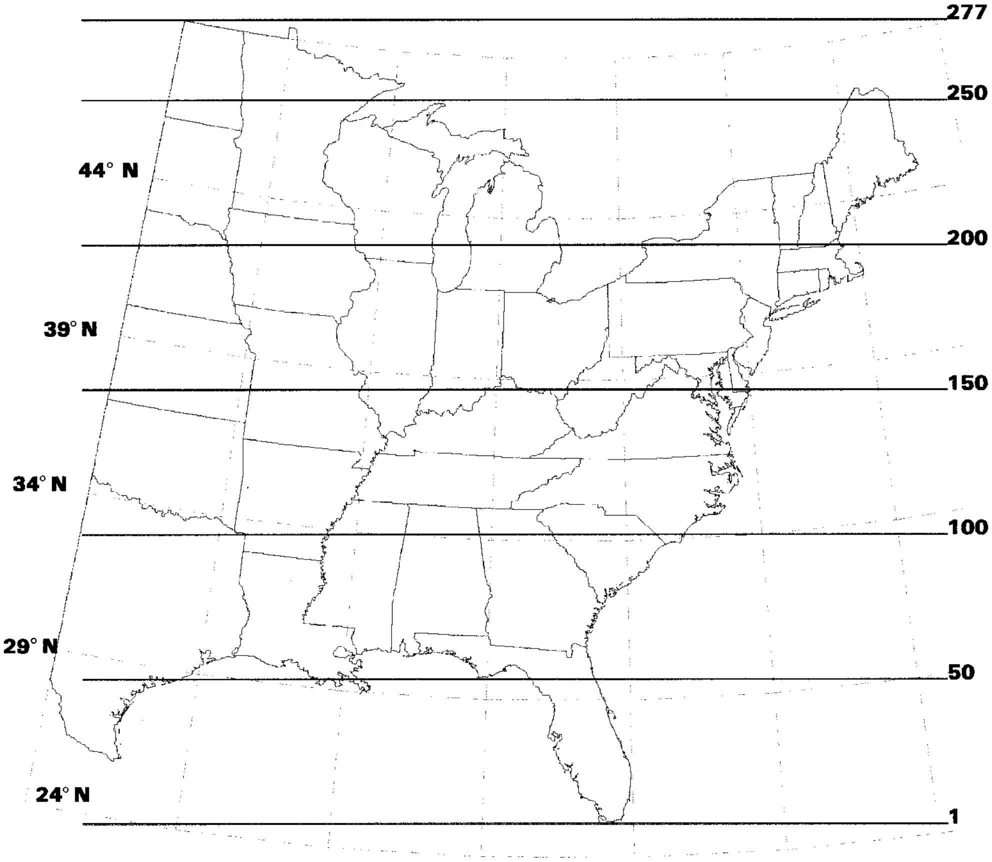


FIG. 1. Study area is the United States east of the 100th meridian. Horizontal lines correspond to the row number for the study area, in increments of 10 km. For example, row 50 corresponds to 500 km above the southern limit of the study area. Latitude and longitude (in degrees) are also given in dashed lines.

> 0, it was assigned to 1, since rounding would have falsely turned species-present counties to species-absent counties.

For each species, average IV per county was calculated by aggregating plot-level information. These values were linked with a county coverage of the United States (ESRI 1992) for mapping into density slices of IV. With these maps, biogeographical characteristics (such as absolute and optimum range) of the species can be visualized. Further details on the methodology, along with a table summarizing the number of plots, number of species, percentage of forest, and dates of the inventories by state, are in Iverson et al. (1996*a*).

Climatic factors.—Monthly means (averaged from 1948 to 1987) of precipitation, temperature, and potential evapotranspiration for the current climate were extracted from a database generated by the USEPA (1993). The data had been interpolated into 10 × 10 km grid cells for the conterminous United States. From these data, we extracted January and July temperatures, calculated annual means, and derived two attributes based on their physiological importance to tree growth for this region: July–August ratio of precipitation to potential evapotranspiration (PET) (the time most prone to drought stress in the eastern United States), and May–September (i.e., growing season) mean temperature. The data were then transformed to county averages via area-weighted averaging.

Two scenarios of future monthly temperature and precipitation under an equilibrium state of twice the present levels of atmospheric CO_2 were used for predictions of potential future species distributions: the Geophysical Fluid Dynamics Laboratory (GFDL) (Wetherald and Manabe 1988) and Goddard Institute of Space Studies (GISS) (Hansen et al. 1988) models, which depict a divergent set of possible outcomes. These GCM output data were prepared by USEPA (1993) into future equilibrium estimates, by 10 × 10 km grid, for monthly precipitation, temperature, and potential evapotranspiration. These variables, along with the derived variables mentioned above, were substituted into the database for predicting potential future species distributions.

Soil factors.—The State Soil Geographic Data Base (STATSGO) was developed by the USDA Soil Conservation Service (now Natural Resource Conservation Service) to help achieve their mandate to collect, store, maintain, and distribute soil survey information for

TABLE 1. County environmental and land-use variables reported for each county and used in the RTA process. Frequency indicates the number of times the variable appeared in the RTA models, while rank-weighted score is the sum of (1/rank in the RTA model) for all 80 species.

Abbreviation	Variable	Frequency	Rank-weight score
Climatic factors			
AVGT	Mean annual temperature (°C)	47	12.0
JANT	Mean January temperature (°C)	115	34.8
JULT	Mean July temperature (°C)	44	9.6
PPT	Annual precipitation (mm)	79	12.9
PET	Potential evapotranspiration (mm/mo)	70	17.6
MAYSEPT	Mean May–September temperature (°C)	30	9.1
JARPPET	July–August ratio of precipitation to PET	27	6.1
Soil factors			
TAWC	Total available water capacity (cm, to 152 cm)	47	6.9
CEC	Cation exchange capacity	58	8.5
PH	Soil pH	45	8.9
PERM	Soil permeability rate (cm/h)	75	15.4
CLAY	Percent clay (<0.002 mm size)	66	12.4
BD	Soil bulk density (g/m^2)	50	5.7
KFFACT	Soil erodibility factor, rock fragments free	92	23.2
OM	Organic matter content (% by mass)	60	13.0
ROCKFRAG	Percent mass of rock fragments 8–25 cm	54	9.7
NO10	Percent passing sieve Number 10 (coarse)	43	6.5
NO200	Percent passing sieve Number 200 (fine)	46	10.5
ROCKDEP	Depth to bedrock (cm)	29	2.8
SLOPE	Soil slope (%)	57	15.7
ORD	Potential soil productivity (m^3 of timber/ha)	61	12.2
ALFISOL	Alfisol (%)	34	9.3
INCEPTSL	Inceptisol (%)	14	1.9
MOLLISOL	Mollisol (%)	30	7.9
SPODOSOL	Spodosol (%)	13	2.6
Land use/cover factors			
FORST.LND	Forest land (%)	54	6.7
CROPS	Cropland (%)	46	13.9
GRAZE.PST	Grazing pasture land (%)	54	8.6
DIST.LND	Disturbed land (%)	35	4.0
Elevation			
MAX.ELV	Maximum elevation (m)	67	18.3
MIN.ELV	Minimum elevation (m)	46	6.6
ELV.CV	Elevation coefficient of variation	46	8.0
Landscape pattern			
ED	Edge density (m/ha)	50	6.4

U.S. lands. STATSGO data contain physical and chemical soil properties for ~18 000 soil series recognized in the Nation (Soil Conservation Service 1991). STATSGO maps were compiled by generalizing more detailed soil-survey maps into soil associations in a scale (1:250 000) more appropriate for regional analysis. We selected 14 soil variables related to tree species' habitat (Table 1). Weighted averages by depth and by area were calculated for county estimates of the soil variables, as detailed in Iverson et al. (1996*a*). Additional soil information was obtained from the GEOECOLOGY databases (Olson et al. 1980), including percentage of the county in each of four soil orders (Table 1).

Land use/cover factors.—GEOECOLOGY (Olson et al. 1980) data were used for estimations of percentage forest, crop, grazing/pasture, and disturbed land (Table 1). These estimates originated from the USDA Soil Conservation Service's National Resources Inventory for 1977.

Elevation.—Maximum, minimum, and variation of elevation were derived for each county from 1:250 000 U.S. Geological Survey (USGS) Digital Elevation Model (DEM) files obtained from the USGS internet site (U.S. Geological Survey 1987).

Landscape pattern.—The 1-km AVHRR forest cover map (U.S. Forest Service 1993) was used to generate statistics on forest-cover pattern by county. Several landscape pattern indices were calculated using FRAGSTATS (McGarigal and Marks 1995), but only edge density was used in the final analysis.

Regression tree analysis

We use regression tree analysis (RTA, also known as classification and regression trees, or CART), to decipher the relationships between environmental factors and species distribution. The methods can either predict classes (classification trees) or average values (regression trees), depending on the nature of the response variable. Developed by Breiman et al. (1984), and used first in the medical field, the methods have only been used in ecological studies since about 1987 (Verbyla 1987). Not incidentally, their use has coincided with the use of geographic information systems, which allow model outputs to be readily mapped across landscapes. Since then, they have been used primarily in classification (e.g., Borchert et al. 1989, Lees and Ritman 1991, Moore et al. 1991, Baker 1993, Lynn et al. 1995), though examples of the ecological use of regression trees are found in Davis et al. (1990) and Michaelsen et al. (1994).

RTA is a recursive data partitioning algorithm that initially splits the data set into two subsets based on a single best predictor variable (the variable that minimizes the variance in the response). It then does the same on each of the subsets and so on recursively. The output is a tree with branches and terminal nodes. The predicted value at each terminal node is the average at that node, which is relatively homogeneous (Chambers and Hastie 1993). RTA is therefore much more flexible in uncovering structure in data that have variables that may be hierarchical, nonlinear, nonadditive, or categorical in nature. RTA is rapidly gaining popularity as a means of devising prediction rules for rapid and repeated evaluation, as a screening method for variables, as a diagnostic technique to assess the adequacy of linear models, and for summarizing large multivariate data sets (Clark and Pregibon 1992).

There are several key advantages to using RTA in our application, which covers such a wide spatial domain, over classical statistical methods (Verbyla 1987, Clark and Pregibon 1992, Breiman et al. 1984, Michaelsen et al. 1994). First, RTA is adept at capturing nonadditive behavior, where relationships between the response variable and some predictor variables are conditional on the values of other predictors. RTA deals with interaction effects by subsetting data without specifying the interaction terms in advance of the statistical analysis (as is necessary in multiple linear regression). For example, in our study, the factors associated with the northern range limits for a species may be quite different from the factors regulating the southern limit of the species. This advantage allows, in effect, a stratification of the country so that some variables may be most related to the IV of species A for a particular region of the country, but a different set of variables may drive its importance elsewhere. Second, numerical and categorical variables can easily be used together and interpreted, because RTA essentially converts continuous data into two categories at each node. The outcome is a set of step functions that provides a better capturing of nonlinear relationships, while also providing a reasonable solution for linear relationships. Last, the variables that operate at large scales are used for splitting criteria early in the model, while variables that influence the response variable locally are used in decision rules near the terminal nodes (Moore et al. 1991). Thus we could expect that broad climatic patterns are captured higher up on the tree, while more local effects (soil, elevation, etc.) determine more local distributional variations. It should, however, be recognized that since our data set is aggregated to a county-level scale, RTA cannot capture the environmental drivers that operate on species at a very fine scale (e.g., individual slopes or valley bottoms).

There are limitations of RTA, however. While RTA may be the most appropriate tool for analyzing data sets with many possibly interacting predictor variables and for separating macro-level and micro-level effects on the response, the response ideally should be approximately normal, since least squares and the group mean are used in deriving the best split (Clark and Pregibon 1992). Even though the IV response in our example more closely resembles a Poisson distribution due to the high frequency of zeros, the effect of long tails is much more confined than in a linear regression model as the regression is local (B. D. Ripley, *personal communication*). Also, since we are mainly interested in variables that are driving the distribution geographically, we believe this is a reasonable approach; transforming the response would complicate the interpretability of the results. We are taking a further step and predicting the effect of a changed climate based on the model. While there is danger of extrapolating the results beyond the model's predictive ability for some species, it does provide a reasonable estimate of the species' potential migration under changed climatic conditions, whose preferences we know a priori.

Prediction of current species importance values.—Regression trees were generated in S-PLUS (Statistical Sciences 1993) for each tree species. Species importance value (IV, based on basal area and number of stems) was the response variable, with the 33 predictor variables (see Table 1). The regression trees were generated on a split data set—a random selection of 80% of the data—so that 20% of the data remained for validation efforts. RTA models were generated after pruning the full tree to 12–20 nodes, depending on the rate of change of deviance explained. When the additional deviance explained was small for added nodes, the RTA model building was stopped. The resulting model was used to generate predictions of IV of each species for each county. While this pruning effort carried some subjectivity, it is the most reasonable approach while evaluating 80 tree species; picking nodes through cross validation by resampling is not without some major limitations (Venables and Ripley 1994).

In addition to the RTA models using all the 33 predictors, we built models using only the seven climatic variables (Table 1). This analysis was done to compare prediction effectiveness with that using edaphic and land use variables. For several species, maps were also generated that depict the counties that fall along particular branches of the RTA tree. The environmental variables most responsible for the predicted IV are shown geographically, which is a major strength of RTA.

The response predicted by RTA for zero values of IV was almost always a fraction <1. Through testing across all species, we determined that predicted IV scores <1.0 were essentially zero and were set as such. Predicted IV scores between 1.0 and 3.0 were classed ''fuzzy'' in that we were not confident in the prediction of these low IV scores. The predictions of IV classes were then output to Arc/Info for mapping, using Unix tools and Arc/Info's Arc Macro Language (ESRI 1993).

Validation/verification of the RTA outputs.—To evaluate the model outputs, a comparison between predicted current and actual (FIA) distributions was made using correlation, verification, and validation processes. Scattergrams and correlations of IV were calculated for each species. Verification, to assess how well the models recreate the distributions with the entire data set, was performed by assessing for each species the number and proportion of counties found in (*a*) both the actual and predicted scenarios, (*b*) only the actual, and (*c*) only the predicted. This allowed calculation of the percent correct assignment $([a/(a + b + c)] \times 100$, hereafter referred to as classification accuracy), and also the calculation of omission errors, where the model failed to predict the presence of the target species even though it was recorded in the FIA data $([a/(a + b)] \times 100$, hereafter referred to as omission accuracy). We were especially interested in the omission accuracy. The error was deemed less serious if the model predicted a county to contain a species that was not recorded because it is quite possible that the FIA sampling may have missed it. FIA attempts to place a plot for about every 2000 ha of forest land; uncommon or habitat-specific species could easily be missed by the plots. A validation comparison was made by using a randomly selected portion of the counties (80%) to predict the IV of the remaining 20% ($n = 424$). Similar calculations of error were then made on this 20% data set.

Prediction of future species importance values.—Once the regression trees were generated, they were used to generate not only predictive maps of current distributions, but also potential future distributions under a scenario of a changed climate. We did this by replacing the climate-related variables in our predictor variable set with those based on the GFDL and GISS models. The replaced variables were (see Table 1 for the description): MAYSEPT, JARPPET, JANT, JULT, AVGT, PET, and PPT. The previously established regression trees then were used with the new predictive variables, and the data output to Arc/Info as before.

Assessment of potential species changes.—We devised several metrics to assess the potential species shifts as a result of the modeled changes in IV of each species. The first metric, change in area, is the difference, in percent, between the predicted current areal extent and the predicted potential future areal extent under the two climate change scenarios. So, a score of 100 means no change, scores <100 represent a contraction of the range, and scores >100 are an expansion of the species range. Because of relatively large uncertainty in the ''fuzzy'' class of predicted IV (1.0–3.0), we took a conservative approach and calculated this metric only for counties with IV > 3.0.

The second metric, change in weighted average of IV, is a weighted (by area of counties) average of IV for all counties calculated for predicted current vs. the two climate change scenarios; as above, a score below 100 indicates the overall importance of the species will decline (though areal extent may or may not decline). In this case, we included the ''fuzzy'' class of predicted IV in the calculation, since county areas with low IV would not contribute much to the overall score.

The third metric is the change in northern and southern range limits. Because we were not interested in spurious shifts out on the tails of the distribution, we statistically identified the range limits for predicted current and future ranges. The country was subdivided into a grid cell network of 10 × 10 km cells; a total of 277 rows, or latitudinal strips, was generated (Fig. 1). The relative IVs were calculated for each row (total IV/total area in row), and box plots were generated, in S-PLUS (Statistical Sciences 1993), for the summed IV for each species. From this distribution, the IV of the first quartile was identified; the first and last row where this IV was exceeded was deemed the northern and southern limit of the distribution, respectively. Shifts in the northern or southern limits were simply calculated by taking the difference between current and projected future limits.

The fourth metric is the change in ecological optimum. The mean of the interquartile range was deemed the ''optimum'' latitude range for the species. Both of the latter metrics used only those areas with predicted IV values >3.0; the ''fuzzy'' class was not included.

Model assumptions and limitations

Here we attempt to state our assumptions explicitly so that progress can continue as uncertainties are reduced. First, uncertainty remains in projected climate change under a doubled CO_2 scenario, especially as it plays out spatially across the continent. The impacts of this uncertainty on our results are reduced by using two scenarios, but changes in estimates of future climate will continue to occur. Second, any time multiple GIS layers from disparate sources and scales are overlaid, errors will propagate through the data (Goodchild and Gopal 1989). This impact is minimized in this study by using a large sampling unit, the county, as the common spatial unit. On the other hand, some counties are very diverse, and some important ecological factors could be averaged out at this scale. For example,

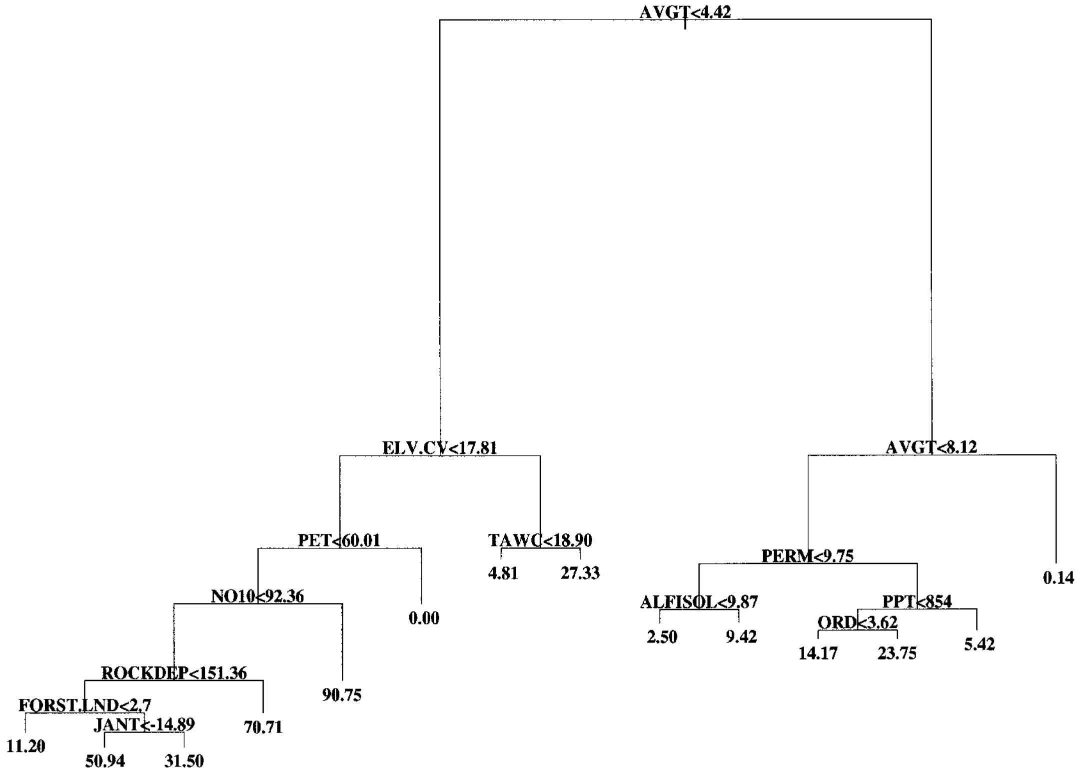


FIG. 2. Regression tree for quaking aspen (*Populus tremuloides*), using a nonuniform tree of 12 nodes. If the rule at the top of a branch is true, follow the left branch; if false, follow the right branch. The numbers at the termination points refer to predicted IV for that particular branch of the model, which is the average IV at that node. The length of the vertical line below each true–false split corresponds to the importance of the variable.

small zones of high elevation, bottomlands, or unique soils, which harbor specialized flora, may be lost in the averaging process. There is also error associated with the FIA sampling of trees; occasionally species that do in fact reside in the county will be missed by the FIA sampling plots. Third, the method described here does not account for changes in physiological and species-interaction effects in the model outputs. Therefore, there is no way to assess changes in competition among the ''new'' species mix, nor is there a way to account for whatever gains in water-use efficiency may accompany elevated CO_2 (Neilson 1995). Fourth, in a criticism of model-based assessments of climate change effects on forests, Loehle and LeBlanc (1996) note that many forest simulation models assume that tree species occur in all environments where it is possible for them to survive, and that they cannot survive outside the climatic conditions of their current range (fundamental vs. realized niche). The RTA models here reduce this problem by considering a wide range of variables and only trying to evaluate *potential* range changes due to climate change. These models assume equilibrium conditions, and that there are no barriers to migration. Finally, RTA does have limitations, and spurious or noncausative relationships will appear, especially when RTA methodology is applied to 80 species without fine-tuning for individual species preferences. Improvement of models may be possible for many of the species, if individual characteristics and spatial trends are taken into account.

RESULTS AND DISCUSSION

Regression trees

Regression trees were generated for each species; an example for quaking aspen (*Populus tremuloides*) is shown in Fig. 2. At the terminal ends of each branch, a predicted IV is presented. In this example, the relatively large importance of mean annual temperature is apparent, for the distance between nodes is in proportion to the variance explained by the variable. The highest predicted importance occurs on the left branch, where a maximum IV of 91 was obtained if the mean annual temperature was <4.4°C, the coefficient of variation of elevation in the county was <17.8% (i.e., the county is homogeneously rather flat), the average potential evapotranspiration was <60.0 mm/mo, and >92.3% of soil can pass a number 10 sieve (i.e., the soils are primarily sands and finer material). Only eight counties matched these criteria. On the other branch, the lowest IV, 0.14, was found for counties that had an average temperature >8.12°C; this condition occurs in 1704 counties. Because we used a cutoff of 1.0 for a species to be considered present, none of the 1704 counties was predicted to have quaking aspen.

The distribution of variables most responsible for the predicted IV for three species shows the additional value of the RTA in that different variables operate in controlling the distribution (Fig. 3). For example, with southern red oak (*Quercus falcata* var. *falcata*), there is essentially no representation of the species in 1222 counties with an average January temperature <0.34°C. In this example, the maximum IV (8.0) is found in 94 counties that have: a January temperature >0.34°C, an average slope in the county exceeding 2.3%, average total water-holding capacity exceeding 19.5 cm, and a maximum elevation >160 m (Fig. 3). The northern band of southern red oak presence is found where January temperature is <3.2°C, indicating that temperature may be the key factor regulating the northern boundary of the species.

For Virginia pine (*Pinus virginiana*), pH is the first controlling variable, with the species found only where pH < 4.35, except for 26 counties with higher pH but with average slopes exceeding 21% (Fig. 3). If the pH criterion is satisfied and January temperatures <0.7°C, then the species is found (IV > 1) only in counties where slopes > 20.8%. This could be a situation where the species can survive colder winters in protected steep valleys or on more southerly exposures. Virginia pine prefers warmer temperatures in January (>0.7°C) but relatively cooler temperatures in July (<25.1°C), unless the maximum elevation in the county exceeds 889 m (Fig. 3). The importance of the species is thus distributed spatially by soil and climate factors.

American beech (*Fagus grandifolia*) reaches its maximum IVs when potential evapotranspiration (PET) is <46.5 mm/mo and when maximum elevation exceeds 663 m, conditions met by 76 counties in the northern Appalachians. For lower elevations in the north, beech can be prevalent if precipitation exceeds 850 mm. For counties with higher PET, beech is mostly found in the high sloping regions of the southern Appalachians (Fig. 3).

As can be seen from the legend of Fig. 3, a combination of climate and edaphic variables was necessary to achieve the best RTA models. This pattern held true for nearly all species. Scores of frequency of occurrence in RTA outputs for all 80 species showed January temperature to be the most influential variable overall. It appeared 115 times at RTA nodes summed across all species (a variable can appear more than once in any given RTA model), and had a rank-weighted score (sum of 1/rank for all species, with rank being the node position of the variable in the model) of 34.8 (Table 1). Next most important was the *K* factor, or wind erodibility of the soil. It relates to texture, being highest with silty soils. By weighted score, the next most important variables, in order, were maximum elevation, potential evapotranspiration, slope, soil permeability, percent cropland, percent organic matter, precipitation, and percent clay (Table 1). Edaphic factors thus occupy 6 of the top 10 positions in relative importance. Most work of this type has ignored edaphic factors (Loehle and LeBlanc 1996).

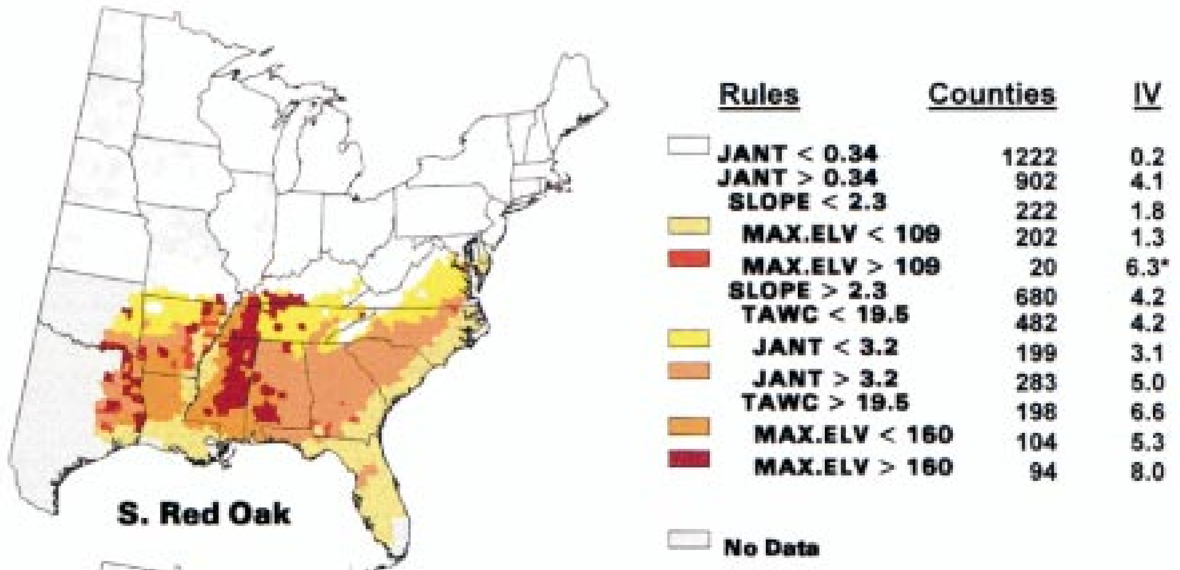
Prediction of current species distributions

Tree models work best if sufficient samples are available (Moore et al. 1991, Clark and Pregibon 1992). Analysis of the verification data set revealed there was a significant correlation between the number of counties for which the target species was recorded in the FIA data and the classification accuracy (Table 2). Those species with larger samples tend to have increased model success based on correlations between predicted and actual IV. Rarer species also tend to have more specific habitat requirements that would be difficult for the coarse, county-level data to capture. Some species that are not so rare, with more specific habitat requirements, also fall into this category. It should be borne in mind that the model was not fine-tuned for individual species preferences, as we were interested in macro-scale comparison among several species. Also, the added benefit of the analysis is that it highlights species that require more individual attention and/or finer resolution data. In light of the above considerations, only those species with a recorded minimum IV of 3.0 in each of at least 100 counties (out of a possible 2124, or 4.7% of the counties) are included in the reporting here. A total of 80 species matches this criterion (Table 2).

Predicted current distributions match FIA data reasonably well for most species. For example, for quaking aspen (*Populus tremuloides*, Fig. 4), the FIA data recorded the species in a total of 338 counties. Total classification accuracy was 71% on the entire data set, and 67% on the 20% validation data set. If only considering error of omission (the RTA model predicted no target species when the FIA sampling recorded it), the accuracies are 81 and 77%, respectively (Table 2). The correlation of IVs (for counties with IV at least 3.0) between predicted and FIA data is 0.81. The species is a generalist, being the most widely dispersed species in the United States, and can grow on a wide variety of soil types (Elias 1980, Perala 1990). The county level of resolution is, therefore, adequate to capture the major environmental variables driving its

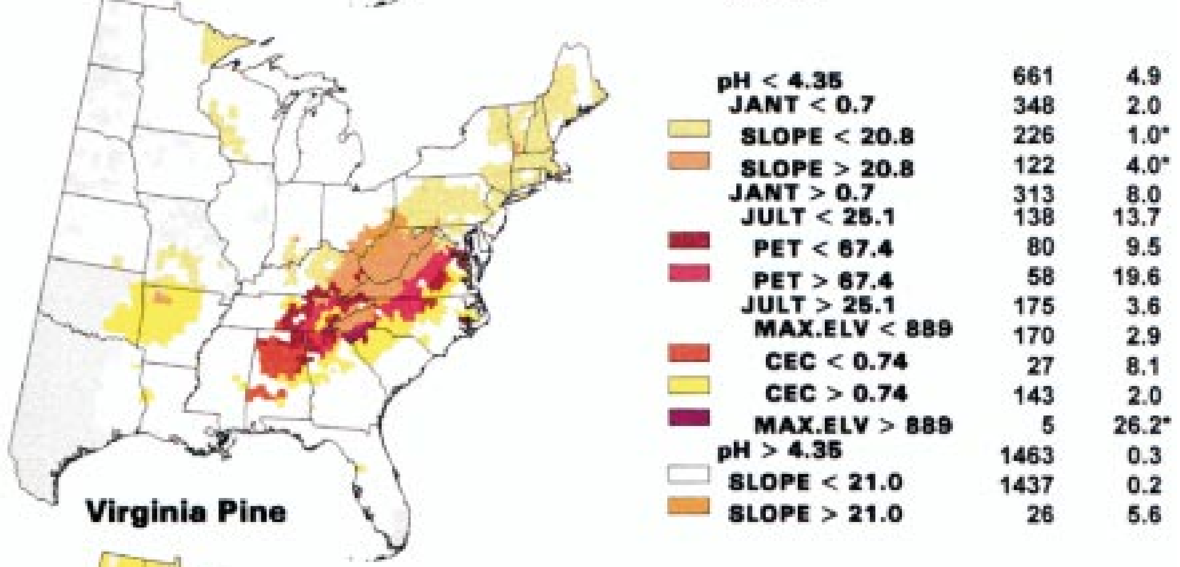
→

FIG. 3. Mapped environmental variables most related to the distribution of three species: (a) southern red oak (*Quercus falcata* var. *falcata*), (b) Virginia pine (*Pinus virginiana*), and (c) American beech (*Fagus grandifolia*). The indented legend shows the hierarchical structure of the data; see Table 1 for definitions of the variables in the first column. The second column is the number of counties that the equation pertains to, and the third column is the average IV for the species for those counties. An asterisk indicates that the branch is a terminal node for the tree.

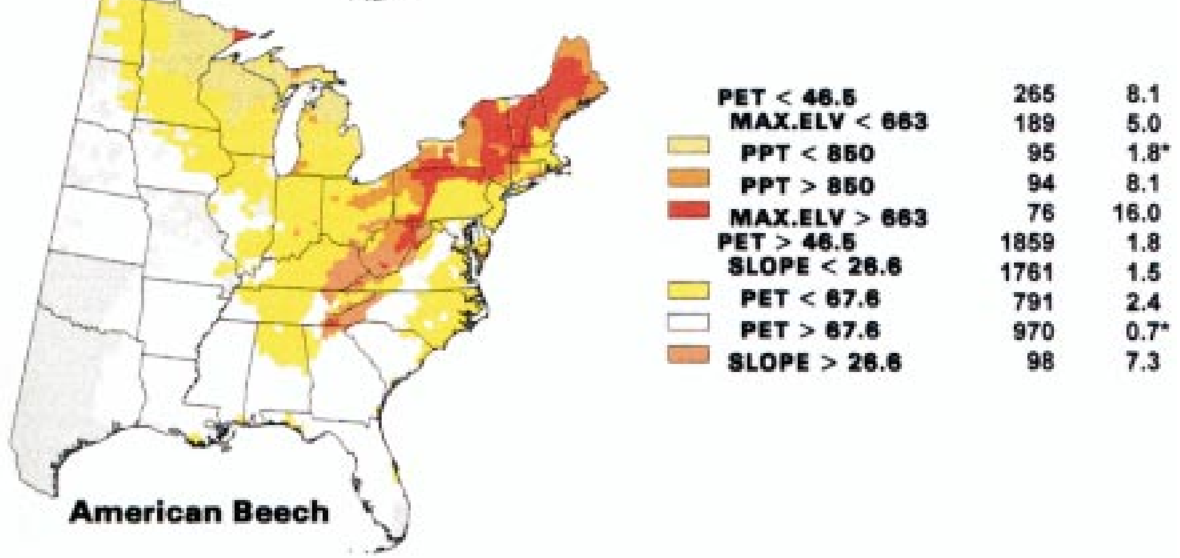


	Rules	Counties	IV
☐	JANT < 0.34	1222	0.2
	JANT > 0.34	902	4.1
	SLOPE < 2.3	222	1.8
▨	MAX.ELV < 109	202	1.3
🟥	MAX.ELV > 109	20	6.3*
	SLOPE > 2.3	680	4.2
	TAWC < 19.5	482	4.2
🟨	JANT < 3.2	199	3.1
🟧	JANT > 3.2	283	5.0
	TAWC > 19.5	198	6.6
🟧	MAX.ELV < 160	104	5.3
🟥	MAX.ELV > 160	94	8.0

☐ No Data



	Rules	Counties	IV
	pH < 4.35	661	4.9
	JANT < 0.7	348	2.0
▨	SLOPE < 20.8	226	1.0*
🟧	SLOPE > 20.8	122	4.0*
	JANT > 0.7	313	8.0
	JULT < 25.1	138	13.7
🟥	PET < 67.4	80	9.5
🟪	PET > 67.4	58	19.6
	JULT > 25.1	175	3.6
	MAX.ELV < 889	170	2.9
🟥	CEC < 0.74	27	8.1
🟨	CEC > 0.74	143	2.0
🟪	MAX.ELV > 889	5	26.2*
	pH > 4.35	1463	0.3
☐	SLOPE < 21.0	1437	0.2
🟧	SLOPE > 21.0	26	5.6



	Rules	Counties	IV
	PET < 46.5	265	8.1
	MAX.ELV < 663	189	5.0
▨	PPT < 850	95	1.8*
🟧	PPT > 850	94	8.1
🟥	MAX.ELV > 663	76	16.0
	PET > 46.5	1859	1.8
	SLOPE < 26.6	1761	1.5
🟨	PET < 67.6	791	2.4
☐	PET > 67.6	970	0.7*
🟧	SLOPE > 26.6	98	7.3

TABLE 2. Verification/validation table for species known from FIA plot data to be present in >100 counties, and with an IV of at least 3.0.

	Verification						Validation				
Species	PF	PP	PB	CA (%)	EOA (%)	CORR	PF	PP	PB	CA (%)	EOA (%)
Abies balsamea	9	45	104	65.8	92.0	0.87	5	6	18	62.1	78.3
Acer negundo	170	250	317	43.0	65.1	0.70	31	61	70	43.2	69.3
Acer pensylvanicum	34	12	55	54.5	61.8	0.72	8	8	15	48.4	65.2
Acer rubrum	53	339	1341	77.4	96.2	0.75	9	69	262	77.1	96.7
Acer saccharinum	161	91	124	33.0	43.5	0.68	35	18	20	27.4	36.4
Acer saccharum	106	238	731	68.0	87.3	0.61	31	41	154	68.1	83.2
Betula alleghaniensis	66	13	86	52.1	56.6	0.77	17	2	21	52.5	55.3
Betula lenta	55	16	88	55.3	61.5	0.73	15	7	18	45.0	54.5
Betula nigra	31	20	32	38.6	50.8	0.19	9	14	1	4.2	10.0
Betula papyrifera	47	18	154	70.3	76.6	0.61	9	13	32	59.3	78.0
Carpinus caroliniana	357	20	95	20.1	21.0	0.30	63	9	20	21.7	24.1
Carya cordiformis	104	49	139	47.6	57.2	0.26	29	12	19	31.7	39.6
Carya glabra	70	9	88	52.7	55.7	0.52	19	6	11	30.6	36.7
Carya ovata	76	171	234	48.6	75.5	0.63	23	21	39	47.0	62.9
Carya sp.	188	196	761	66.5	80.2	0.64	42	28	149	68.0	78.0
Carya tomentosa	47	18	84	56.4	64.1	0.55	10	11	14	40.0	58.3
Celtis laevigata	68	12	52	39.4	43.3	0.80	14	15	14	32.6	50.0
Celtis occidentalis	72	221	351	54.5	83.0	0.73	27	45	67	48.2	71.3
Cercis canadensis	108	60	108	39.1	50.0	0.43	34	17	12	19.0	26.1
Cornus florida	176	109	776	73.1	81.5	0.56	44	30	139	65.3	76.0
Crataegus sp.	153	86	168	41.3	52.3	0.59	30	27	41	41.8	57.7
Diospyros virginiana	161	13	58	25.0	26.5	0.55	36	7	6	12.2	14.3
Fagus grandifolia	236	87	308	48.8	56.6	0.63	38	34	68	48.6	64.2
Fraxinus americana	206	150	612	63.2	74.8	0.65	47	31	123	61.2	72.4
Fraxinus nigra	56	18	94	56.0	62.7	0.57	12	6	15	45.5	55.6
Fraxinus pennsylvanica	139	389	452	46.1	76.5	0.81	38	82	78	39.4	67.2
Fraxinus sp.	90	35	108	46.4	54.5	0.36	14	14	13	31.7	48.1
Gleditsia triacanthos	126	52	109	38.0	46.4	0.52	27	16	19	30.6	41.3
Ilex opaca	88	8	61	38.9	40.9	0.85	20	4	1	4.0	4.8
Juglans nigra	231	102	205	38.1	47.0	0.60	37	28	50	43.5	57.5
Juniperus virginiana	120	322	287	39.4	70.5	0.57	22	73	60	38.7	73.2
Liquidambar styraciflua	85	92	689	79.6	89.0	0.75	16	21	120	76.4	88.2
Liriodendron tulipifera	172	144	563	64.1	76.6	0.65	26	31	109	65.7	80.7
Maclura pomifera	72	38	95	46.3	56.9	0.49	16	19	20	36.4	55.6
Magnolia virginiana	54	20	124	62.6	69.7	0.58	11	10	15	41.7	57.7
Morus rubra	100	38	52	27.4	34.2	0.77	22	5	8	22.9	26.7
Nyssa aquatica	59	9	36	34.6	37.9	0.84	8	5	5	27.8	38.5
Nyssa biflora	44	36	193	70.7	81.4	0.77	8	8	29	64.4	78.4
Nyssa sylvatica	96	201	675	69.4	87.5	0.40	24	32	118	67.8	83.1
Ostrya virginiana	364	63	130	23.3	26.3	0.57	73	21	33	26.0	31.1
Oxydendrum arboreum	87	49	233	63.1	72.8	0.66	18	17	42	54.5	70.0
Pinus echinata	154	38	321	62.6	67.6	0.73	27	24	67	56.8	71.3
Pinus elliottii	39	45	176	67.7	81.9	0.86	8	4	33	73.3	80.5
Pinus palustris	36	60	169	63.8	82.4	0.71	5	9	34	70.8	87.2
Pinus resinosa	55	29	78	48.1	58.6	0.67	8	8	17	51.5	68.0
Pinus strobus	132	59	177	48.1	57.3	0.72	29	11	34	45.9	54.0
Pinus taeda	68	86	591	79.3	89.7	0.75	4	22	108	80.6	96.4
Pinus virginiana	83	101	212	53.5	71.9	0.71	32	18	31	38.3	49.2
Platanus occidentalis	159	29	76	28.8	32.3	0.38	36	17	12	18.5	25.0
Populus deltoides	147	113	142	35.3	49.1	0.82	42	27	22	24.2	34.4
Populus grandidentata	107	5	70	38.5	39.5	0.71	27	5	12	27.3	30.8
Populus tremuloides	57	41	240	71.0	80.8	0.81	16	10	52	66.7	76.5
Prunus serotina	392	208	557	48.1	58.7	0.73	59	80	129	48.1	68.6
Quercus alba	130	411	1130	67.6	89.7	0.59	34	71	199	65.5	85.4
Quercus coccinea	134	117	249	49.8	65.0	0.47	36	9	30	40.0	45.5
Quercus falcata var. *falcata*	89	93	443	70.9	83.3	0.41	25	19	77	63.6	75.5
Quercus falcata var. *pagodaefolia*	35	21	77	57.9	68.8	0.59	18	10	4	12.5	18.2
Quercus laurifolia	54	22	166	68.6	75.5	0.71	6	6	33	73.3	84.6
Quercus macrocarpa	95	109	211	50.8	69.0	0.72	18	47	44	40.4	71.0
Quercus marilandica	71	19	78	46.4	52.3	0.76	15	11	17	39.5	53.1
Quercus muehlenbergii	91	12	59	36.4	39.3	0.59	21	10	8	20.5	27.6
Quercus nigra	80	45	421	77.1	84.0	0.62	21	10	66	68.0	75.9
Quercus palustris	55	16	46	39.3	45.5	0.44	13	3	6	27.3	31.6
Quercus phellos	128	16	65	31.1	33.7	0.75	19	1	9	31.0	32.1
quercus prinus	161	27	265	58.5	62.2	0.68	22	14	60	62.5	73.2
Quercus rubra	161	256	857	67.3	84.2	0.64	35	45	179	69.1	83.6

TABLE 2. Continued.

	Verification						Validation				
Species	PF	PP	PB	CA (%)	EOA (%)	CORR	PF	PP	PB	CA (%)	EOA (%)
Quercus stellata	89	312	410	50.6	82.2	0.86	8	48	90	61.6	91.8
Quercus velutina	133	311	692	60.9	83.9	0.76	29	75	143	57.9	83.1
Robinia pseudoacacia	182	26	125	37.5	40.7	0.33	43	20	24	27.6	35.8
Salix nigra	164	13	42	19.2	20.4	0.65	29	18	9	16.1	23.7
Salix sp.	75	9	28	25.0	27.2	0.56	15	7	5	18.5	25.0
Sassafras albidum	183	143	331	50.4	64.4	0.49	40	17	59	50.9	59.6
Taxodium distichum	40	54	75	44.4	65.2	0.82	14	9	6	20.7	30.0
Taxodium distichum var. *nutans*	21	21	68	61.8	76.4	0.78	4	9	16	55.2	80.0
Thuja occidentalis	26	16	75	64.1	74.3	0.77	1	9	15	60.0	93.8
Tilia americana	119	147	258	49.2	68.4	0.67	19	53	64	47.1	77.1
Tsuga canadensis	57	48	148	58.5	72.2	0.70	15	6	28	57.1	65.1
Ulmus alata	51	82	257	65.9	83.4	0.69	18	20	50	56.8	73.5
Ulmus americana	207	169	674	64.2	76.5	0.68	58	36	130	58.0	69.1
Ulmus rubra	83	284	445	54.8	84.3	0.42	26	62	68	43.6	72.3
Ulmus sp.	161	7	65	27.9	28.8	0.54	26	12	15	28.3	36.6
Mean				52.24	63.93	0.64				45.59	59.15

Note: PF = number of counties present in FIA data only; PP = number of counties present in predictive model only; PB = number of counties present in both; CA = classification accuracy (PB/[PB + PF + PP] × 100); EOA = error of omission accuracy (PB/[PB + PF] × 100); CORR = correlation between actual and predicted IV.

distribution, and conditions represented by county averages are adequate to model the species.

For flowering dogwood (*Cornus florida*) (Fig. 5), the model has classification accuracies of 73 and 65% for the full and 20% data set, and omission accuracies of 82 and 76%, respectively (Table 2). This species too is a generalist, but favors lighter soils with good drainage (McLemore 1990).

For all 80 species, classification accuracies ranged widely, from 19% for black willow (*Salix nigra*) to 80% for sweetgum (*Liquidambar styraciflua*); the average was 52% in the full verification data set (Table 2). The omission accuracies were somewhat better, ranging from 20 to 96%, with an average accuracy of 63%. In general, the more specialized the species is with respect to edaphic conditions, the less accuracy in the RTA model predictions. In fact, in nearly all situations where the accuracy was less than ∼40%, the species is known to be a habitat specialist, preferring bottomlands, alkaline areas, or disturbed systems. These are not attributes readily captured in the coarse-resolution data set used here. Several poorly classified species, including *Morus rubra, Nyssa aquatica, Platanus occidentalis, Populus grandidentata, Salix nigra,* and *Taxodium distichum,* are all bottomland species. Bottomland habitats would occupy a small minority of most counties, and county-resolution data would not be expected to consistently capture the appropriate information in the RTA process. Lower classification accuracies were also apparent in taxa that were reported at the genus level (for example, *Salix* sp. and *Ulmus* sp., Table 2). Because these taxa include a number of different species, with varying habitat requirements, the RTA would be less likely to uncover precise trends. An exception is *Carya* sp., in which several species of hickory have similar habitat requirements.

Species that showed high classification and omission accuracies (greater than ∼70% classification accuracy or 80% omission accuracy), on the other hand, tended to be capable of occupying a large variety of habitats within their range of distribution. For example, *Acer rubrum* is one of the most common species in eastern North America (Elias 1980, Golet et al. 1993). *Liquidambar styraciflua, Nyssa sylvatica, Pinus taeda, Quercus alba,* and *Q. rubra* are also generalist species, occupying a wide variety of sites within their ranges (Elias 1980). County-level environmental data are much more likely to represent conditions for these species than the specialist species.

When the RTA analysis using only climatic variables as inputs was compared to the results described above, we found the inclusion of edaphic and land-use variables to be vitally important for many species. For example the climate-only model failed for *Taxodium distichum,* whose distribution is mainly driven by elevation and permeability. For 70 of the 80 species, the correlation between actual and predicted IV was improved with the addition of the extra variables. In addition, when using only climate variables, one could cause the resultant model to be overly sensitive to climate under changed climate scenarios. These results indicate the importance of assessing edaphic constraints in the prediction of species shifts following climate change.

Prediction of potential future species importance and area

Projected potential species distributions, following equilibrium of predicted climate changes, show major

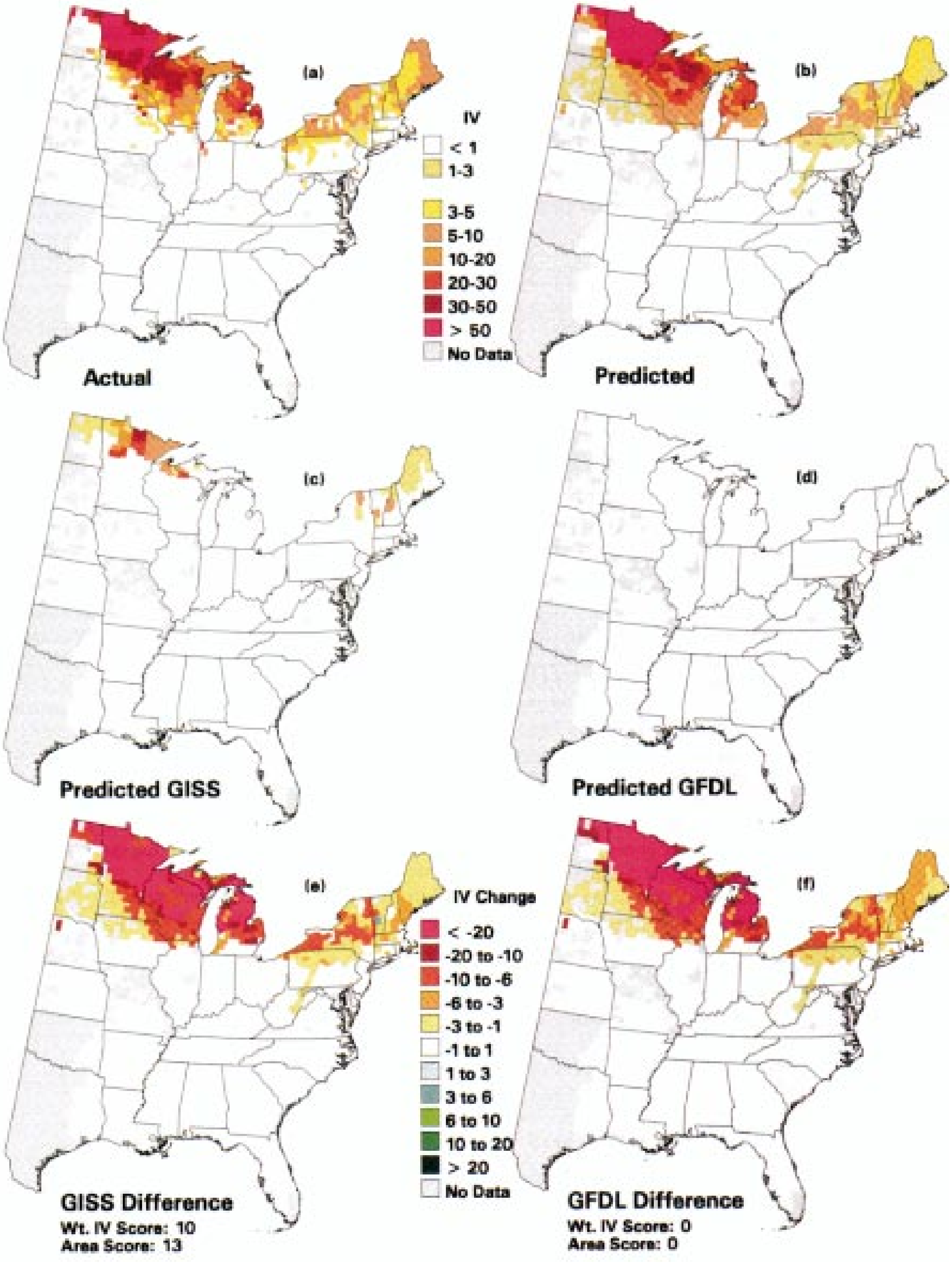


FIG. 4. Example model outputs for quaking aspen (*Populus tremuloides*), including (a) actual county importance value (IV) as calculated from FIA data; (b) predicted current IV from the RTA model; (c) predicted potential future IV after climate change according to the GISS GCM; (d) predicted potential future IV after climate change according to the GFDL GCM; (e) difference between predicted current and predicted future IV according to the GISS model; and (f) difference between predicted current and predicted future IV according to the GFDL model. This example shows a species with the potential to contract its range and importance in the United States under climate change.

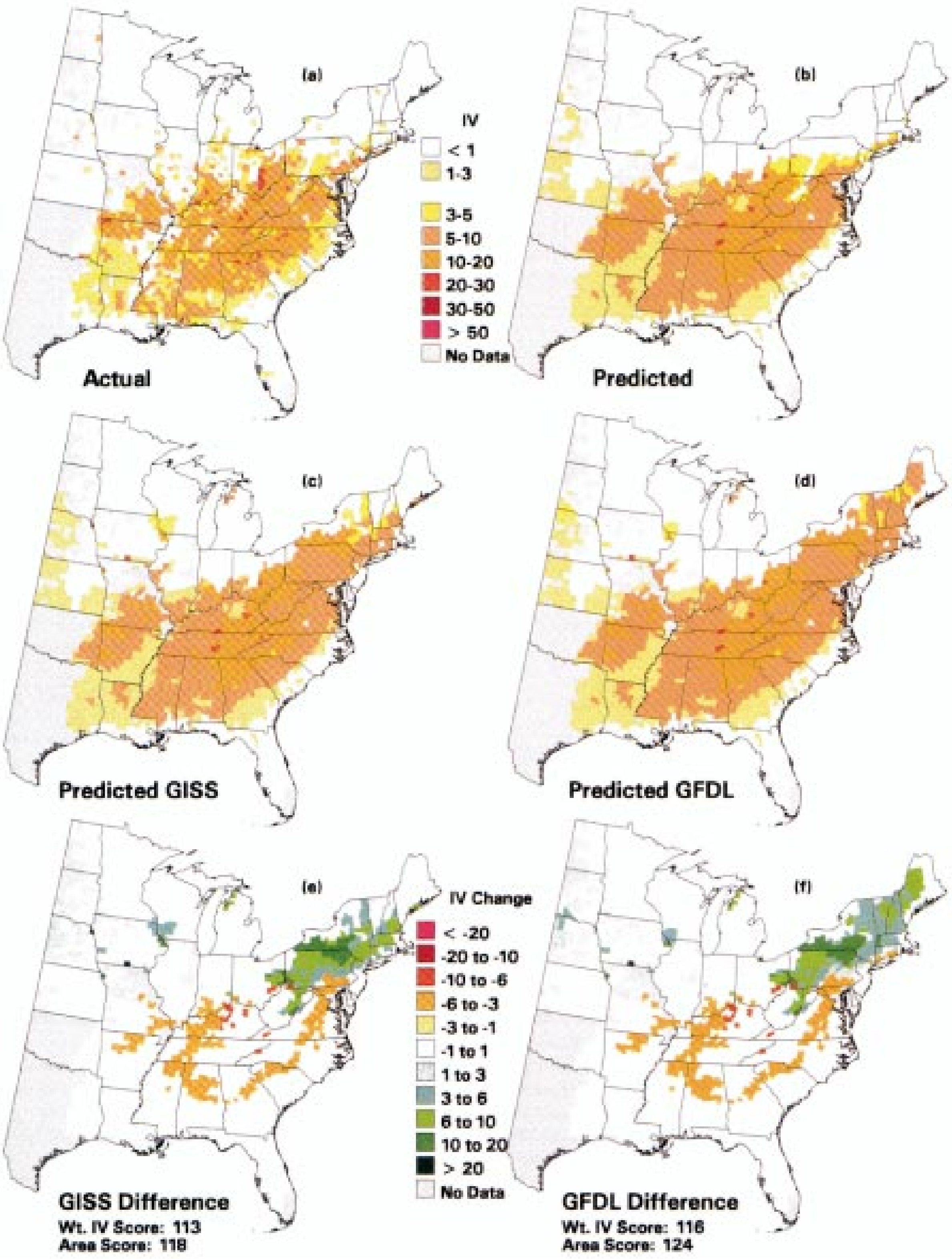


FIG. 5. Example model outputs for flowering dogwood (*Cornus florida*), including (a) actual county importance value (IV) as calculated from FIA data; (b) predicted current IV from the RTA model; (c) predicted potential future IV after climate change according to the GISS GCM; (d) predicted potential future IV after climate change according to the GFDL GCM; (e) difference between predicted current and predicted future IV according to the GISS model; and (f) difference between predicted current and predicted future IV according to the GFDL model. This example shows a species with the potential to expand its range and importance under climate change.

TABLE 3. Predicted potential changes of area and weighted average importance values, after GISS and GFDL, with twofold increases in CO_2 levels. Scores above 100 correspond to increases; those less than 100 correspond to decreases.

	IV score		Area score			IV score		Area score	
Species	GISS	GFDL	GISS	GFDL	Species	GISS	GFDL	GISS	GFDL
Abies balsamea	1	0	3	0	*Pinus echinata*	149	146	123	119
Acer negundo	101	101	100	100	*Pinus elliottii*	148	149	165	162
Acer pensylvanicum	27	25	20	17	*Pinus palustris*	187	170	208	204
Acer rubrum	65	34	100	100	*Pinus resinosa*	7	0	4	0
Acer saccharinum	104	104	98	98	*Pinus strobus*	135	134	92	84
Acer saccharum	8	0	9	0	*Pinus taeda*	180	179	158	158
Betula alleghaniensis	27	0	53	0	*Pinus virginiana*	141	167	108	106
Betula lenta	51	49	42	41	*Platanus occidentalis*	157	156	127	130
Betula papyrifera	14	0	9	0	*Populus deltoides*	119	210	112	155
Carpinus caroliniana	117	129	230	289	*Populus grandidentata*	2	0	2	0
Carya cordiformis	101	88	93	86	*Populus tremuloides*	10	0	13	0
Carya glabra	37	37	10	10	*Prunus serotina*	52	47	7	0
Carya ovata	120	81	87	93	*Quercus alba*	97	102	77	69
Caya sp.	94	81	87	73	*Quercus coccinea*	90	64	105	63
Carya tomentosa	176	358	154	315	*Quercus falcata* var. *falcata*	230	229	206	206
Celtis laevigata	329	624	278	1031	*Quercus falcata* var. *pagodaefolia*	151	148	159	154
Celtis occidentalis	225	228	72	65	*Quercus laurifolia*	149	148	120	121
Cercis canadensis	144	191	180	252	*Quercus macrocarpa*	61	55	48	49
Cornus florida	113	116	118	124	*Quercus marilandica*	180	955	184	851
Crataegus sp.	8	5	6	3	*Quercus muehlenbergii*	197	212	233	259
Diospyros virginiana	196	217	330	350	*Quercus nigra*	158	171	127	127
Fagus grandifolia	24	11	30	21	*Quercus palustris*	32	36	28	33
Fraxinus americana	63	60	58	52	*Quercus phellos*	199	216	167	177
Fraxinus nigra	44	46	58	63	*Quercus prinus*	101	98	112	112
Fraxinus pennsylvanica	112	116	100	100	*Quercus rubra*	68	52	72	70
Fraxinus sp.	91	120	40	135	*Quercus stellata*	237	889	105	199
Gleditsia triacanthos	160	155	119	113	*Quercus velutina*	94	108	107	91
Ilex opaca	75	78	52	52	*Robinia pseudoacacia*	94	87	98	109
Juglans nigra	247	717	143	313	*Salix nigra*	100	100	100	100
Juniperus virginiana	362	579	242	325	*Salix* sp.	105	105	100	100
Liquidambar styraciflua	113	113	153	154	*Sassafras albidum*	80	63	70	44
Liriodendron tulipifera	86	83	97	96	*Taxodium distichum*	102	102	100	100
Maclura pomifera	279	526	202	370	*Taxodium distichum* var. *nutans*	628	557	316	280
Magnolia virginiana	253	242	181	169	*Thuja occidentalis*	0	0	0	0
Morus rubra	114	100	109	100	*Tilia americana*	31	25	20	2
Nyssa aquatica	79	79	75	75	*Tsuga canadensis*	60	66	47	48
Nyssa biflora	133	133	100	100	*Ulmus alata*	359	898	210	472
Nyssa sylvatica	120	99	104	104	*Ulmus americana*	98	99	100	100
Ostrya virginiana	61	61	29	30	*Ulmus rubra*	101	184	87	103
Oxydendrum arboreum	90	84	78	75	*Ulmus* sp.	117	117	173	173

shifts for many species (Table 3). For example, quaking aspen is projected to move north of the United States boundary under the GFDL scenario, and nearly so with the GISS scenario (Fig. 4), while flowering dogwood is projected to move to the northeast (Fig. 5). For most species, area and weighted average IV shift together, though *Acer rubrum* is predicted to keep the same distribution but decrease markedly in importance. A summary of species predictions shows that approximately equal numbers of species would decrease or would increase in IV and area importance, according to this analysis (Fig. 6). The figure shows that 27 to 36 species would increase by at least 10% (≥110 on the relative IV or area scale), while 30 to 34 species would decrease by at least 10% (≤90). The remaining species would change little in overall weighted importance or area. Further, most species behave similarly, regardless of the GCM model being used, as 28–33 species increased in both GISS and GFDL models, while 31 species decreased in both scenarios. Only one species, *Carya ovata*, showed a reversal of trend between GCM scenarios, where IV is projected to increase under GISS and decrease under GFDL.

Comparisons of potential changes in distribution and abundance were made with published examples for a few species; this type of work has been done for only a few eastern North American species. General agreement was found. For example, Jacobson and Dieffenbacker-Krall (1995) predicted that white pine (*Pinus strobus*) would be favored, while spruce–fir would be decreased under a climate change. We found a 35% increase predicted in area-weighted IV for white pine (even though it is likely to move substantially northward), but that balsam fir (*Abies balsamea*) would be nearly eliminated from the United States as it migrated northward (Table 3). Similarly, Flannigan and Wood-

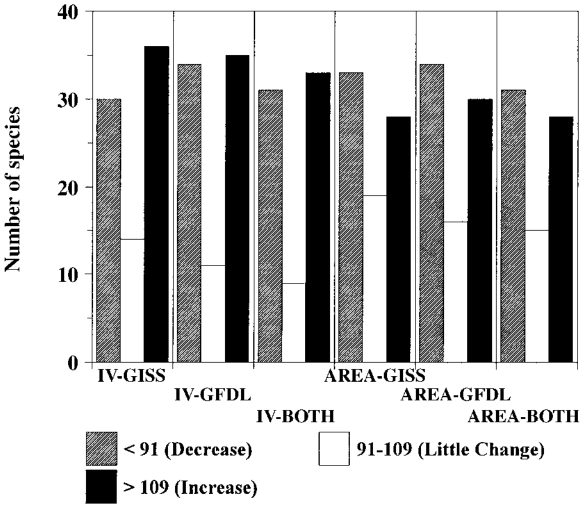


FIG. 6. Number of species showing decreases or increases of importance value (IV) or area for the two GCM scenarios evaluated. The total number of species is <80 for the ''Both'' categories, because those species that fall in different classes between GCM scenarios are not tallied.

ward (1994) predicted red pine (*Pinus resinosa*) to migrate 600–800 km to the northeast, but with an increase in volume per unit area. We predict that the species may migrate completely out of the United States into Canada.

Overpeck et al. (1991) predicted the above general patterns for northern pines, as well as large increases in oak abundance in the northern Great Lakes and New England (also found by us for black, northern red, and white oak; *Quercus velutina, Q. rubra, and Q. alba,* respectively). They also predicted a severe northern shift for birch, especially with the GFDL over the GISS global change scenario. Again, these results agree with ours for paper birch (*Betula papyrifera*). Finally, Overpeck et al. (1991) predicted a large northward expansion for southern pines, as exemplified by loblolly pine (*Pinus taeda*). Joyce et al. (1990) also report a predicted expansion for loblolly. Our results concur by predicting an 80% increase in area-weighted IV, and a 58% increase in range area (Table 3).

Predicted changes in potential species importance by county

Predicted changes in major species importance for any county can be generated with the RTA outputs (Table 4). For example, in Vinton County in southern Ohio, the GISS climate projections show that, among 15 species projected to decline, *Acer saccharum* and *Prunus serotina* would decline sharply, while *Oxydendrum arboreum* and *Quercus alba* would increase in importance. An additional 14 species are projected to change very little (less than one IV unit, on average) under the changed climate.

TABLE 4. Predicted change in importance values (IV) for tree species from Vinton County, Ohio (GISS model only).

Species	Change
Acer saccharum	−14.5
Prunus serotina	−10.0
Crataegus sp.	−7.1
Fagus grandifolia	−4.9
Fraxinus americana	−3.6
Ulmus rubra	−3.3
Pinus virginiana	−2.9
Cercis canadensis	−2.6
Platanus occidentalis	−1.7
Robinia pseudoacacia	−1.7
Asimina triloba	−1.3
Carpinus caroliniana	−1.2
Carya glabra	−1.1
Malus sp.	−1.1
Populus grandidentata	−1.0
Acer negundo	0
Acer rubrum	0
Carya sp.	0
Cornus florida	0
Fraxinus pennsylvanica	0
Liriodendron tulipifera	0
Nyssa sylvatica	0
Ostrya virginiana	0
Quercus coccinea	0
Quercus prinus	0
Quercus rubra	0
Quercus velutina	0
Sassafras albidum	0
Ulmus americana	0
Quercus alba	4.0
Oxydendrum arboreum	7.5

Predicted changes in potential species boundaries and optima

Estimates of southern limit, northern limit, and zone of ecological optimum, along with the estimated IV at the ecological optimum, were calculated using quartile distributions (Table 5). Though this statistical method of calculating limits is flawed for some species by outlier counties having predicted distributions according to the models, it gives us a metric for quantifying potential migration for most species. Because each number corresponds to a latitudinal strip of 10 km starting from the southern tip of Florida, we can begin to estimate potential shifts in the northern and southern limits. According to this analysis, four species (*Betula papyrifera, Pinus resinosa, Populus grandidentata,* and *Thuja occidentalis*) are projected by the GISS GCM model to have their southern optimum move north of the United States border, while five additional species (*Abies balsamea, Acer saccharum, Betula alleghaniensis, Populus tremuloides,* and *Prunus serotina*) are projected to disappear according to the GFDL model. Shifts of the southern optima are also apparent for several species that do stay in the United States: *Acer pensylvanicum, Betula lenta, Carya glabra, Celtis occidentalis, Cercis canadensis, Cornus florida, Crataegus* sp., *Diospyros virginiana, Oxydendrum arboreum, Pinus virginiana, Quercus muehlenbergii, Q. palustris, Tilia americana,* and *Tsuga canadensis* show a sizable

TABLE 5. Calculated north–south ranges, shifts, and estimated importance values due to GISS and GFDL model forecasts. Scores of −99 indicate that the species is projected to become absent in the United States, while a score of 208 indicates that the species abuts the Canadian border, and a score of 70 indicates the species abuts the Gulf of Mexico.

	Southern optimum				Northern optimum			
Species	FIA	Pred.	GISS	GFDL	FIA	Pred.	GISS	GFDL
Abies balsamea	191	135	199	−99	208	208	204	−99
Acer negundo	71	76	76	76	208	208	208	208
Acer pensylvanicum	118	143	166	166	208	208	203	203
Acer rubrum	104	104	70	70	208	208	208	199
Acer saccharinum	95	118	76	76	208	208	208	208
Acer saccharum	120	110	148	−99	208	208	208	−99
Betula alleghaniensis	109	146	191	−99	208	208	208	−99
Betula lenta	120	144	157	157	202	208	208	208
Betula papyrifera	179	188	−99	−99	208	207	−99	−99
Carpinus caroliniana	70	70	70	70	206	205	191	208
Carya cordiformis	96	140	140	140	208	208	208	208
Carya glabra	86	129	153	153	191	179	179	179
Carya ovata	132	110	110	110	208	208	208	207
Carya sp.	73	73	82	81	201	204	208	206
Carya tomentosa	76	76	76	76	194	208	208	208
Celtis laevigata	70	70	70	70	134	128	208	208
Celtis occidentalis	85	113	140	140	208	208	208	208
Cercis canadensis	86	104	121	121	183	182	208	208
Cornus florida	70	70	89	89	201	186	201	197
Crataegus sp.	70	153	194	185	208	208	203	203
Diospyros virginiana	70	70	80	80	161	156	208	208
Fagus grandifolia	71	103	102	102	208	208	208	163
Fraxinus americana	71	70	70	70	208	208	208	208
Fraxinus nigra	150	181	185	185	208	208	208	208
Fraxinus pennsylvanica	70	70	70	70	208	208	208	208
Fraxinus sp.	70	70	70	70	157	170	170	170
Gleditsia triacanthos	74	81	81	81	203	197	206	206
Ilex opaca	70	111	99	99	161	160	147	147
Juglans nigra	110	70	70	81	207	198	208	208
Juniperus virginiana	70	85	70	70	208	208	208	208
Liquidambar styraciflua	70	70	70	70	173	173	202	205
Liriodendron tulipifera	74	92	94	94	189	208	208	208
Maclura pomifera	93	70	70	71	189	202	201	208
Magnolia virginiana	70	70	70	70	168	168	126	138
Morus rubra	95	144	144	144	206	201	197	201
Nyssa aquatica	70	77	77	77	139	138	138	138
Nyssa biflora	70	70	70	70	143	195	160	162
Nyssa sylvatica	70	70	70	70	191	177	204	204
Ostrya virginiana	73	80	80	80	208	208	208	205
Oxydendrum arboreum	81	83	99	99	163	152	175	175
Pinus echinata	70	70	70	70	168	129	190	191
Pinus elliottii	70	70	70	70	115	91	127	127
Pinus palustris	70	70	70	70	114	111	154	180
Pinus resinosa	157	176	−99	−99	208	208	−99	−99
Pinus strobus	104	104	104	104	208	208	208	208
Pinus taeda	70	70	70	70	153	153	171	176
Pinus virginiana	89	75	91	93	169	204	187	190
Platanus occidentalis	72	86	86	86	191	171	177	202
Populus deltoides	128	145	145	145	208	208	208	208
Populus grandidentata	152	135	−99	−99	208	208	−99	−99
Populus tremuloides	162	135	205	−99	208	208	208	−99
Prunus serotina	70	93	188	−99	208	208	208	−99

TABLE 5. Extended.

Latitudinal optimum				IV at optimum latitude			
FIA	Pred.	GISS	GFDL	FIA	Pred.	GISS	GFDL
200	180	202	−99	4.8	5.4	4.0	−99
145	144	144	144	11.0	6.0	6.0	6.0
170	177	182	182	6.2	7.4	3.0	3.0
156	156	147	127	20.2	15.6	8.3	4.9
161	167	163	159	12.8	13.0	14.6	14.8
164	161	183	−99	16.2	12.8	10.0	−99
169	182	200	−99	6.0	6.4	4.6	−99
164	173	184	184	8.5	9.1	8.1	7.4
198	198	−99	−99	6.6	11.0	−99	−99
138	147	128	139	4.9	5.9	4.6	4.6
161	174	174	174	6.0	4.9	5.0	4.9
152	150	165	165	6.5	6.7	5.8	5.8
174	167	167	167	10.5	6.2	6.6	6.5
133	130	137	140	10.3	8.6	9.3	8.3
137	134	145	146	6.8	6.1	6.1	6.1
99	97	143	139	12.7	20.1	21.7	14.0
156	160	174	178	14.7	10.0	39.6	44.2
140	143	170	170	5.3	4.3	4.6	4.6
129	124	145	143	8.7	8.0	8.4	8.3
147	182	198	194	7.8	8.5	12.7	8.7
116	116	148	149	4.8	6.3	6.6	6.4
155	164	144	132	9.3	9.8	7.6	6.2
156	163	159	160	10.7	11.1	9.8	10.1
185	195	196	196	6.8	7.2	7.7	7.5
145	137	140	140	15.0	10.4	11.5	11.8
117	118	122	117	5.4	3.6	4.1	3.5
150	164	173	173	7.7	6.9	14.1	14.3
117	134	123	123	7.2	10.7	6.2	6.2
167	135	140	150	8.5	5.5	21.5	27.8
151	150	139	139	13.5	8.3	12.6	13.7
114	118	128	132	18.6	18.3	13.0	13.6
134	141	142	142	9.3	9.8	9.0	8.4
146	143	134	144	12.2	15.6	18.0	18.7
114	109	97	101	5.4	5.2	10.8	11.0
162	173	169	173	10.1	16.9	20.1	16.9
105	103	103	103	6.4	8.2	7.3	7.3
101	123	112	113	12.3	9.3	17.6	17.5
132	122	132	132	7.0	5.3	6.6	5.4
143	164	147	153	6.7	9.3	8.9	16.0
119	119	137	137	6.7	6.1	10.0	9.6
108	103	121	120	11.7	13.2	16.7	17.7
90	79	95	98	12.6	13.1	17.9	19.0
93	92	104	121	9.6	7.2	8.9	10.3
185	194	−99	−99	7.5	6.9	−99	−99
156	155	156	156	10.4	10.7	15.2	15.5
109	110	112	121	35.4	35.2	41.0	36.9
126	126	137	140	11.6	7.5	11.6	14.5
134	127	137	140	6.2	5.5	9.3	9.6
173	177	175	177	27.1	26.4	21.8	28.8
183	185	−99	−99	6.6	9.0	−99	−99
188	186	206	−99	9.1	7.9	8.7	−99
139	153	198	−99	8.0	7.7	10.3	−99

TABLE 5. Continued.

Species	Southern optimum				Northern optimum			
	FIA	Pred.	GISS	GFDL	FIA	Pred.	GISS	GFDL
Quercus alba	70	70	70	70	145	141	182	182
Quercus coccinea	70	70	73	71	158	158	196	198
Quercus falcata var. *falcata*	100	92	95	95	208	208	208	208
Quercus falcata var. *pagodaefolia*	92	92	99	99	201	204	198	196
Quercus laurifolia	70	70	70	70	116	113	131	138
Quercus macrocarpa	148	156	156	156	208	208	208	208
Quercus marilandica	70	74	79	90	171	159	208	208
Quercus muehlenbergii	105	106	127	127	200	173	208	208
Quercus nigra	70	70	70	70	154	120	154	171
Quercus palustris	123	133	173	172	204	191	190	190
Quercus phellos	70	70	70	70	151	128	191	208
Quercus prinus	93	93	89	89	204	187	208	208
Quercus rubra	110	106	109	137	208	208	208	208
Quercus stellata	74	74	77	86	175	157	208	208
Quercus velutina	105	93	109	109	208	208	208	208
Robinia pseudoacacia	87	106	106	106	207	198	206	198
Salix nigra	123	164	164	164	208	207	207	207
Salix sp.	70	70	70	70	207	123	122	122
Sassafras albidum	79	95	95	95	206	208	182	208
Taxodium distichum	70	70	70	70	123	78	108	121
Taxodium distichum var. *nutans*	70	70	70	70	145	193	193	193
Thuja occidentalis	194	144	−99	−99	208	208	−99	−99
Tilia americana	110	150	182	175	208	208	205	205
Tsuga canadensis	109	109	128	128	208	208	208	208
Ulmus alata	74	70	70	70	145	146	208	208
Ulmus americana	83	70	70	70	208	208	208	208
Ulmus rubra	78	80	70	70	208	208	208	208
Ulmus sp.	76	73	70	70	206	206	206	206

Note: FIA = Forest Inventory Analysis data; Pred. = predicted current; predicted future with GISS = Goddard Institute of Space Sciences model; predicted future with GFDL = Geophysical Fluid Dynamics Laboratory model. Numbers correspond to row numbers shown in Fig. 1.

(>100 km) northward shift in their southern boundaries (Table 5). Of course, because of tree longevity and remnant refugia, it would take centuries for these shifts to be realized (Loehle and LeBlanc 1996).

For a large portion of the species, the northern optimum abuts the Canadian border so an estimate of potential migration is not possible (row number 208 for northern optimum in Table 5). However, for the species where the northern optimum is projected to stay south of the Canadian border, sizable shifts in northern optima are apparent. For example, the following species are projected to shift their northern limit by at least 100 km to the north: *Celtis laevigata, Cercis canadensis, Cornus florida, Diospyros virginiana, Liquidambar styraciflua, Nyssa sylvatica, Oxydendrum arboreum, Pinus echinata, P. elliottii, P. palustris, P. taeda, Quercus alba, Q. coccinea, Q. laurifolia, Q. marilandica, Q. muehlenbergii, Q. nigra, Q. phellos, Q. stellata,* and *Ulmus alata.* Many of these species do not concomitantly shift their southern limits northward. Differing environmental factors are related to the range boundaries on the north vs. south. This geographic shift in variable importance shows the power of the RTA analysis; for general linear or general additive methods, the variables have to operate equally everywhere.

Because calculations of the ecological optimum latitude are not as prone to outliers and boundary effects, they may provide the best indicator of projected species movement (Table 5). A total of 36 species are projected to have their zone of maximum IV migrate at least 100 km north. Of these, seven are estimated to move in excess of 250 km: *Cercis canadensis, Prunus serotina, Quercus coccinea, Q. marilandica, Q. stellata, Tsuga canadensis,* and *Ulmus alata.* Interestingly, five taxa are projected to have their ecological optima shift south: *Carpinus caroliniana, Fagus grandifolia, Juniperus virginiana, Magnolia virginiana,* and *Sassafras albidum.* In these cases, there seems to be a relative constriction of range to the higher elevations of the southern Appalachians.

Estimated IV for the ecological optima are also presented for current and future projections (Table 5). Some species are projected to significantly increase in importance at their ecological optima, including *Celtis occidentalis, Gleditsia triacanthos, Juglans nigra, Magnolia virginiana, Nyssa biflora, Pinus elliottii, Pinus strobus, Quercus stellata, Taxodium distichum, Tilia americana,* and *Ulmus alata.* On the other hand, significant decreases in importance are projected for

TABLE 5. Extended.

Latitudinal optimum				IV at optimum latitude			
FIA	Pred.	GISS	GFDL	FIA	Pred.	GISS	GFDL
107	104	121	120	5.3	5.3	5.0	5.2
111	111	136	139	6.7	5.5	7.0	6.9
154	150	155	154	13.1	9.5	11.9	13.7
146	143	147	145	7.0	5.3	5.5	8.1
91	90	105	107	6.3	6.5	10.8	10.9
180	183	182	182	18.6	20.7	15.3	15.3
119	115	150	146	7.5	8.8	10.2	12.6
149	147	170	170	6.9	7.9	8.3	8.4
103	92	108	117	8.5	9.0	9.4	9.9
162	162	181	180	7.9	7.3	8.1	8.9
108	94	129	135	5.2	7.1	8.1	7.9
142	145	155	152	12.1	13.8	12.9	12.8
161	157	172	172	8.6	6.5	5.7	4.6
120	115	146	146	13.6	9.9	27.4	42.3
156	151	163	154	10.0	6.8	7.5	11.0
153	151	151	146	6.5	9.4	9.4	9.6
173	184	184	184	10.9	20.3	20.3	20.3
129	98	94	94	9.3	13.2	14.7	14.7
150	148	138	145	6.9	5.9	6.2	6.3
88	73	88	90	4.2	5.0	17.1	15.5
105	110	110	110	7.1	6.4	5.0	5.0
201	188	−99	−99	8.6	7.0	−99	−99
165	179	193	190	7.0	6.6	13.5	16.6
159	159	189	189	7.8	6.3	9.3	9.8
105	108	136	144	9.2	6.8	11.5	16.7
149	141	141	140	13.5	10.9	10.6	10.7
156	144	142	135	8.0	5.0	9.1	13.2
137	138	131	131	6.7	8.9	8.9	8.9

several species, including *Acer rubrum, Liquidambar styraciflua,* and *Quercus macrocarpa.*

CONCLUSIONS

The work described here differs from most in that it operates at the species level over a large geographic region for most of the major species in the eastern United States. Regression tree analysis has been shown to be a valuable tool to improve understanding of species–environment relations for 80 tree species. Space has limited the information portrayed for each species, but the key variables correlated with the present IV distributions of each species have been identified. The operating variables differ geographically, so that, as we have shown, the northern range boundary can be related to different variables than the southern range boundary. Accuracy of prediction of current IVs varied widely among species. Species more related to disturbance or specialized habitats area did not model as well as those regionally controlled by environmental variables. Model improvements could be expected, especially for specialist species, with finer scale input data and fine tuning of individual models.

RTA was used here to predict *potential* migrations of trees under a climate scenario associated with a twofold increase in the level of atmospheric CO_2. We emphasize that potential future ranges presented here do not represent forecasts, but rather an indication of the potential impact on species distributions. With our analysis of potential effects, we show that 27–36 species would significantly increase in area and/or weighted IV, while an additional 30–34 species would decrease by at least 10%, following equilibrium after a changed climate. Nearly half of the species assessed (36 out of 80) showed the potential for the ecological optima to shift at least 100 km to the north, including seven that could move >250 km. Depending on the GCM used, 4–9 species would potentially move out of the United States. Results obtained here compare favorably with those obtained by other researchers (for some species). However, only a few eastern U.S. species had been assessed for changes in potential distribution and abundance prior to this study.

Historic rates of migration (~10–50 km/100 yr) will not likely occur with current fragmented habitat. Even at historic rates, many species would not reach the potential distributions predicted here within the next century without major intervention. In work underway in a related research effort (e.g., Schwartz 1996; L. R. Iverson, A. Prasad, and M. W. Schwartz, *unpublished* *manuscript*), we are investigating more realistic migration scenarios based on historic species migration rates and actual landscapes.

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LITERATURE CITED

Baker, F. A. 1993. Classification and regression tree analysis for assessing hazard of pine mortality caused by *Heterobasidion annosum.* Plant Disease **77**:136–139.

Bonan, G. B., and L. Sirois. 1992. Air temperature, tree growth, and the northern and southern range limits to *Picea mariana.* Journal of Vegetation Science **3**:495–506.

Booth, T. H. 1990. Mapping regions climatically suitable for particular tree species at the global scale. Forest Ecology and Management **36**:47–60.

Borchert, M., F. W. Davis, J. Michaelsen, and L. D. Oyler. 1989. Interactions of factors affecting seedling recruitment of blue oak (*Quercus douglasii*) in California. Ecology **70**: 389–404.

Box, E. O., D. W. Crumpacker, and E. D. Hardin. 1993. A climatic model for location of plant species in Florida, U.S.A. Journal of Biogeography **20**:629–644.

Breiman, L., J. Freidman, R. Olshen, and C. Stone. 1984. Classification and regression trees. Wadsworth, Belmont, California, USA.

Burton, P. J., and S. G. Cumming. 1995. Potential effects of climatic change on some western Canadian forests, based on phenological enhancements to a patch model of forest succession. Water Air and Soil Pollution **82**:401–414.

Chambers, J. M., and T. J. Hastie. 1993. Statistical models in S. Chapman and Hall, New York, New York, USA.

Clark, L. A., and D. Pregibon. 1992. Tree-based models. Pages 377–419 *in* T. J. Hastie, editor. Statistical models in S. Wadsworth, Pacific Grove, California, USA.

Davis, F. W., J. Michaelsen, R. Dubayah, and J. Dozier. 1990. Optimal terrain stratification for integrating ground data from FIFE. Pages 11–15 *in* Symposium on FIFE, First ISLSCP Field Experiment. American Meteorological Society, Boston, Massachusetts, USA.

Davis, M. B., and C. Zabinski. 1992. Changes in geographical range resulting from greenhouse warming: effects on biodiversity in forests. Pages 297–308 *in* R. L. Peters and T. E. Lovejoy, editors. Global warming and biological diversity. Yale University Press, New Haven, Connecticut, USA.

Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology; relevant scales in space and time. Landscape Ecology **2**:23–44.

Dyer, J. M. 1995. Assessment of climatic warming using a model of forest species migration. Ecological Modelling **79**:199–219.

Elias, T. S. 1980. The complete trees of North America. Van Nostrand Reinhold, New York, New York, USA.

ESRI. 1992. ArcUSA 1:2M, user's guide and data reference. Environmental Systems Research Institute, Redlands, California, USA.

———. 1993. Arc/Info GRID command reference. Environmental Systems Research Institute, Redlands, California, USA.

Ertsen, A. C. D., J. W. Frens, J. W. Nieuwenhuis, and M. J. Wassen. 1995. An approach to modelling the relationship between plant species and site conditions in terrestrial ecosystems. Landscape and Urban Planning **31**:143–151.

Flannigan, M. D., and F. I. Woodward. 1994. Red pine abundance: current climatic control and responses to future warming. Canadian Journal of Forest Research **24**:1166–1175.

Foley, J. A., I. C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance and vegetation dynamics. Global Biogeochemical Cycles **10**:603–628.

Franklin, J. 1995. Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. Progress in Physical Geography **19**:474–499.

Golet, F. C., A. J. K. Calhoun, W. R. DeRagon, D. J. Lowry, and A. J. Gold. 1993. Ecology of red maple swamps in the glaciated northeast: a community profile. Biological Report 12, U.S. Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA.

Goodchild, M. F., and S. Gopal. 1989. Accuracy of spatial databases. Taylor and Francis, Bristol, Pennsylvania, USA.

Hansen, J., I. Fung, A. Lacis, D. Rind, S. Lebedeff, and R. Ruedy. 1988. Global climate changes as forecast by Goddard Institute for Space Studies three-dimensional model. Journal of Geophysical Research **93**:9341–9364.

Hansen, M. H., T. Frieswyk, J. F. Glover, and J. F. Kelly. 1992. The eastwide forest inventory data base: users manual. U.S. Forest Service North Central Forest Experiment Station General Technical Report **NC-151**.

Hobbs, Richard J. 1994. Dynamics of vegetation mosaics: can we predict responses to global change? Ecoscience **1**(4):346–356.

Hughes, L., E. M. Cawsey, and M. Westoby. 1996. Climatic range sizes of Eucalyptus species in relation to future climate change. Global Ecology and Biogeography Letters **5**: 23–29.

Huntley, B., P. Berry, W. Cramer, and A. P. McDonald. 1995. Modelling present and potential future ranges of some European higher plants using climate response surfaces. Journal of Biogeography **22**:967–1001.

Iverson, L. R., M. E. Dale, C. T. Scott, and A. Prasad. 1997. A GIS-derived integrated moisture index to predict forest composition and productivity in Ohio forests. Landscape Ecology **12**:331–348.

Iverson, L. R., A. Prasad, and C. T. Scott. 1996*a.* Preparation of forest inventory and analysis (FIA) and state soil geographic data base (STATSGO) data for global change research in the eastern United States. Pages 209–214 *in* J. Hom, R. Birdsey, and K. O'Brian, editors. Proceedings, 1995 meeting of the Northern Global Change Program. U.S. Forest Service Northeastern Forest Experiment Station General Technical Report **NE-214**.

Iverson, L. R., C. T. Scott, M. Dale, and A. M. G. Prasad. 1996*b.* Development of an integrated moisture index for predicting species composition. Pages 101–116 *in* M. Kohl and G. Z. Gertner, editors. Caring for the forest: research in a changing world. Statistics, mathematics, and computers. Swiss Federal Institute for Forest, Snow and Landscape Research, Birmensdorf, Switzerland.

Jacobson, G. L., Jr., and A. Dieffenbacker-Krall. 1995. White pine and climate change: insights from the past. Journal of Forestry **93**:39–42.

Jacobson, G. L., Jr., T. Webb III, and E. C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. Pages 277–288 *in* W. F.

Ruddiman and H. E. Wright, Jr., editors. North America and adjacent oceans during the last deglaciation. Geological Society of America, Boulder, Colorado. USA.

Jelinski, D. E., and J. Wu. 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecology **11**:129–140.

Joyce, L. A., M. A. Fosberg, and J. M. Comanor. 1990. Climate change and America's forests. U.S. Forest Service Rocky Mountain Forest and Range Experiment Station General Technical Report GTR **RM-187**.

Kattenberg, A., F. Giorgi, H. Grassl, G. A. Meehl, J. F. B. Mitchell, R. J. Stouffer, T. Tokioka, A. J. Weaver, and T. M. L. Wigley. 1996. Climate models—projections of future climate. Pages 285–357 *in* J. T. Houghton et al., editors. Climate Change 1995: the science of climate change. Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Lees, B. G., and K. Ritman. 1991. Decision-tree and rule-induction approach to integration of remotely sensed and GIS data in mapping vegetation in disturbed or hilly environments. Environmental Management **15**:823–831.

Loehle, C., and D. LeBlanc. 1996. Model-based assessments of climate change effects on forests: a critical review. Ecological Modelling **90**:1–31.

Lynn, H., C. L. Mohler, S. D. DeGloria, and C. E. McCulloch. 1995. Error assessment in decision-tree models applied to vegetation analysis. Landscape Ecology **10**:323–335.

Mackey, B. G., and R. A. Sims. 1993. A climatic analysis of selected boreal tree species, and potential responses to global climate change. World Resource Review **5**:469–487.

Malanson, G. P. 1993. Comment on modeling ecological response to climatic change. Climatic Change **23**:95–105.

McGarigal, K., and B. J. Marks. 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. U.S. Forest Service Pacific Northwest Research Station General Technical Report **PNW-GTR-351**.

McGuire, A. D., L. A. Joyce, D. W. Kicklighter, J. M. Melillo, G. Esser, and C. J. Vorosmarty. 1993. Productivity response of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. Climatic Change **24**:287–310.

McLemore, B. F. 1990. *Cornus florida* L. Flowering dogwood. Pages 278–283 *in* R. M. Burns and B. H. Honkala, coordinators. Silvics of North America. Volume 2: Hardwoods. U.S. Forest Service Agriculture Handbook **654**.

Melillo, J. M., J. Borchers, J. Chaney, H. Fisher, S. Fox, and A. Haxeltine. 1995. Vegetation/ecosystem modeling and analysis project: comparing biogeography and biogeochemistry models in a continental-scale study of terrestrial ecosystem responses to climate change and CO2 doubling. Global Biogeochemical Cycles **9**:407–437.

Michaelsen, J., D. S. Schimel, M. A. Friedl, F. W. Davis, and R. C. Dubayah. 1994. Regression tree analysis of satellite and terrain data to guide vegetation sampling and surveys. Journal of Vegetation Science **5**:673–686.

Moore, D. E., B. G. Lees, and S. M. Davey. 1991. A new method for predicting vegetation distributions using decision tree analysis in a geographic information system. Journal of Environmental Management **15**:59–71.

Neilson, R. P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications **5**:362–385.

Neilson, R. P., and D. Marks. 1994. A global perspective of regional vegetation and hydrologic sensitivities from climatic change. Journal of Vegetation Science **5**:715–730.

Olson, R. J., C. J. Emerson, and M. K. Nungesser. 1980. Geoecology: a county-level environmental data base for the conterminous United States. Publication Number 1537. Oak Ridge National Laboratory Environmental Sciences Division, Oak Ridge, Tennessee, USA.

Overpeck, J. T., P. J. Bartlein, and T. Webb III. 1991. Potential magnitude of future vegetation change in Eastern North America: comparisons with the past. Science **254**: 692–695.

Perala, D. A. 1990. *Populus tremuloides* Michx. Quaking aspen. Pages 555–569 *in* R. M. Burns and B. H. Honkala, coordinators. Silvics of North America. Volume 2: Hardwoods. U.S. Forest Service Agriculture Handbook **654**.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography **19**:117–134.

Rastetter, E. B. 1996. Validating models of ecosystem response to global change. BioScience **46**:190–197.

Reed, R. A., R. K. Peet, M. W. Palmer, and P. S. White. 1993. Scale dependence of vegetation–environment correlation: a case study of a North Carolina piedmont woodland. Journal of Vegetation Science **4**:329–340.

Schwartz, M. W. 1996. Assessing the ability of plants to respond to climatic change through distribution shifts. Pages 184–191 *in* J. Hom, R. Birdsey, and K. O'Brian, editors. Proceedings, 1995 meeting of the Northern Global Change Program. U.S. Forest Service Northeastern Forest Experiment Station General Technical Report **NE-214**.

Soil Conservation Service. 1991. State soil geographic data base (STATSGO) data users guide. USDA Soil Conservation Service Miscellaneous Publication **1492**.

Starfield, A. M., and F. S. Chapin, III. 1996. Model of transient changes in arctic and boreal vegetation in response to climate and land use change. Ecological Applications **6**: 842–864.

Statistical Sciences. 1993. S-PLUS guide to statistical and mathematical analysis, version 3.2. StatSci, Seattle, Washington, USA.

U.S. Geological Survey. 1987. Digital elevation models: U.S. Geological Survey data user's guide 5. U.S. Geological Survey, Reston, Virginia, USA.

U.S. Forest Service. 1993. Forest type groups of the United States. Map produced by Z. Zhu, D. L. Evans, and K. Winterberger. Southern Forest Experiment Station, Starksville, Mississippi, USA.

USEPA. 1993. EPA-Corvallis model-derived climate database and 2 × CO2 predictions for long-term mean monthly temperature, vapor pressure, wind velocity and potential evapotranspiration from the Regional Water Balance Model and precipitation from the PRISM model, for the conterminous United States. Digital raster data on a 10 × 10 km, 470 × 295 Albers Equal Area grid, in ''Image Processing Workbench'' format. USEPA Environmental Research Laboratory. Corvallis, Oregon, USA.

Venables, W. N., and B. D. Ripley. 1994. Modern applied statistics with S-Plus. Springer-Verlag, New York, New York, USA.

Verbyla, D. L. 1987. Classification trees: a new discrimination tool. Canadian Journal of Forest Research **17**:1150–1152.

Webb, T., III, and P. J. Bartlein. 1992. Global changes during the last 3 million years: climatic controls and biotic responses. Annual Review of Ecology and Systematics **23**: 141–173.

Wetherald, R. T., and S. Manabe. 1988. Cloud feedback processes in a general circulation model. Journal of Atmospheric Science **45**:1397–1415.

Woodward, F. I. 1992. Tansley Review no. 41. Predicting plant responses to global environmental change. New Phytologist **122**:239–251.