Predicting Potential Changes in Suitable Habitat and Distribution by 2100 for Tree Species of the Eastern United States

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Abstract

We predict current distribution and abundance for tree species present in eastern North America, and subsequently estimate potential suitable habitat for those species under a changed climate with $2 \times CO_2$. We used a series of statistical models (i.e., Regression Tree Analysis (RTA), Multivariate Adaptive Regression Splines (MARS), Bagging Trees (BT) and Random Forests (RF)) via our model, DISTRIB, for this purpose. These techniques were evaluated on several tree species, and advantages and disadvantages of each method were noted. RF provides the best prediction maps of potential suitable habitat. Overall, a combination of RTA, BT, and RF may yield the best information and most interpretable maps of suitable habitat. Using these tools, we provide statistics on potential changes in suitable habitat for 135 tree species of eastern North America.

A suitable habitat does not guarantee the presence of a species, as many barriers for the species still exist before it will be able to colonize that new suitable habitat. Dispersal ability, abundance of the colonizing species, and the nature of fragmented landscapes also influence migration and are modeled with our cellular automata model, SHIFT. For each cell outside a species' current boundary, SHIFT creates an estimate of the probability that each unoccupied cell will become colonized over 100 years. By evaluating the probability of colonization within the potential "new" suitable habitat, we can estimate the proportion of new habitat that might be colonized within a century. This proportion is low ($<15\%$) for five example species, suggesting that there is a serious lag between the potential movement of suitable habitat and the potential for the species to migrate into the new habitat. However, humans could accidentally or purposefully alter the migration rates of species by physically moving the propagules.

Key words: Climate change, Eastern United States, Migration, Predictive vegetation mapping, Tree species distribution.

1. Introduction

Evidence continues to mount on the impacts that climate change is already having on more and more species over several parts of the world (e.g., Fitter and Fitter, 2002; Cotton, 2003). Many more possible impacts are being projected via models (Matsui et al., 2004), conceptual models of species functions and habits (Ohsawa et al., 1998), and field studies (Tanaka et al., 1998). Though much uncertainty remains in these predictions and observations, convergence of paleoecological evidence (e.g., Davis and Zabinski, 1992; DeHayes et al., 2000) and modeling (Kirilenko et al., 2000) indicates that tree species will eventually undergo radical changes in distribution. It is also clear that these changes in distribution will occur unevenly among species so that the various species that combine to form a community will come together in different combinations under climate change (Webb and Bartlein, 1992).

Our group has been involved for some time in statistically modeling the potential change in habitat

for common tree species in eastern United States. We initially built 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, 2000). This model was run at the scale of the county and used 33 climatic, edaphic, and land-use variables. In a current update of this work, we use 20×20 km cells rather than counties, have an updated predictor and response variable set, and have extended the number of species modeled from 80 to 135 tree species found in the eastern United States. We also use the new tools, Bagging Trees (BT) and Random Forest (RF), to improve predictive capability in the statistical models (Prasad *et al.,* in press; Iverson *et al.,* 2004a).

We also have used a cellular automata model, SHIFT, to simulate migration of selected tree species over a 100 year period (Schwartz, 1993; Iverson *et al.,* 1999b, 2004b; Schwartz *et al.,* 2001). The output of SHIFT yields a colonization probability of the species over that period of time. The intersection of DISTRIB, which maps the suitability of the habitat, and SHIFT, which maps the probability of migration over 100 years, yields a map of feasible locations for new colonization under various scenarios of climate change (Iverson *et al.,* 2004c).

In this paper, we summarize this total process to facilitate a step-by-step procedure definition. We also summarize the areal estimates of DISTRIB output for 135 species using Random Forest and provide some results of SHIFT and the DISTRIB-SHIFT combined for five representative species.

2. Materials and Methods

Here we provide a step-by-step procedure for conducting the research imbedded within DISTRIB and SHIFT. Table 1 presents the steps, with further explanation described here or referred to in earlier papers.

2.1 DISTRIB

The primary data source for this effort was the USDA Forest Service's Forest Inventory and Analysis (FIA) plot which were numbered over 100,000 for the study area and which included data on nearly 3 million trees (Miles *et al.,* 2001). From these plots, importance values for 135 tree species were calculated based equally on the relative number of stems and the relative basal area in each plot (Iverson and

Prasad, 1998). The plot data were averaged to yield IV estimates for each 20×20 km cell for each species. Species were included if they were native and had at least 50 cells of occupancy based on the FIA data, so that several quite rare species are included. Other data, including 3 land use, 1 fragmentation, 5 climate, 5 elevation, 9 soil classes, and 12 soil property variables, were acquired from various agencies and data clearinghouses to provide the 35 predictor variables listed in Table 2. For future climate, we used two general circulation model outputs: the Canadian Climate Centre (CCC) model (Boer *et al.,* 2000) and the Hadley Climate Centre model (Mitchell *et al.,* 1995).

Four statistical processes were performed in this effort. Regression Tree Analysis (RTA) constructs a set of decision rules (a regression tree) on 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). This was the primary tool used in our earlier work (Iverson and Prasad, 1998; Iverson *et al.,* 1999a; Prasad and Iverson, 1999). It has advantages over general linear models in uncovering hidden structures in data, in enabling the mapping of influential predictors, for allowing inclusion of related predictor variables, and for allowing interactions and non-linearities among variables. However, among other disadvantages, it may suffer from an unstable output (i.e., a small change in data can produce a quite different tree).

Multivariate Adaptive Regression Splines (MARS) is similar but handles continuous variables better in that the discontinuous branching at tree nodes in RTA is replaced by continuous smooth functions in MARS (Freidman, 1991; Prasad and Iverson, 2000). However, these functions are sometimes excessively guided by the local nature of the data, rendering it a poor method for predictive modeling.

Bagging Trees (BT) uses the RTA technique but creates multiple training sets by resampling with replacement (bootstrap resampling with 63% of the data selected in each sample) 50 times. These multiple, perturbed trees then are averaged to form a single predictive model (Breiman, 1996).

Random Forest (RF) is a new data-mining technique designed to produce very accurate predictions that do not overfit the data (Breiman, 2001). RF is very similar to BT in that bootstrap samples are

Table 1. Steps of DISTRIB, SHIFT, and the two combined.

DISTRIB (For >100 species with at least 100 cells of occurrence in the eastern U.S.)
Model preparation
1a. Create 20×20 km grid of eastern United States (east of 100th meridian)
2a. Calculate importance value (IV) by plot from FIA data (based on number of stems and basal area)
2b. Summarize importance value by 20×20 km cell
3a. Prepare predictor variables from source data (see Table 2)
3b. Calculate weighted averages for each predictor variable by cell
Model runs
4a. Run Regression Tree Analysis (RTA) to estimate IV from predictors
4b. Run Multivariate Adaptive Regression Splines (MARS) to estimate current IV distribution
4c. Run Bagging Trees (BT) to evaluate stability of 50 individual runs of regression tree analysis using a random 2/3 subset sample
4d. Run Random Forest (RF) to create current estimates of IV from 1,000 perturbated trees (random 2/3 sample and random 15 predictor variables)
4e. Run Random Forest using future scenarios of climate to estimate future IV (suitable habitat)
Outputs
5a. Map outputs of RF for current and potential future suitable habitats
5b. Compare actual (Forest Inventory and Analysis data) maps to predicted current maps
   i. Correlation
   ii. Kappa
   iii. Fuzzy Kappa (Hagen, 2003)
5c. Evaluate relative importance of variables using report outputs from RF
5d. Assess stability of model by calculating variability among multiple trees derived from Bagging Trees
5e. Assess variable relationships, scale of influence, and geographic location of predictors with RTA tree diagrams and maps

SHIFT (for small subset of species that do not reach the Canada border)
Model preparation
6a. Digitize/edit Little (1971, 1977) boundaries of tree distribution
6b. Smooth IV (derived in #2 above) via inverse distance weighting to 1 km resolution for gap filling and matching with Little's atlas boundaries
6c. Create mapped estimate of forest habitat density per 1 km cell
6d. Create 80% random forest map for model calibration
6e. Research species generation times
Model runs
7a. Run trials with 80% random forest map to calibrate migration rate to 50 km/century

7b. Run SHIFT for 100-year migration, using parameters uncovered from trial runs
Outputs
8a. Map estimated probability of colonization after 100 years
8b. Calculate areas of potentially colonized forest, by several probability levels

DISTRIB-SHIFT (for the subset of species)
Processing
9a. Intersect DISTRIB maps with SHIFT maps
Outputs
10a. Calculate percentage of new suitable habitat (DISTRIB) potentially inhabited following 100 years of simulated migration (SHIFT), at 2, 20, and 50% probability of colonization

drawn to construct multiple trees; however in RF, each tree is also grown with a randomized subset of predictor variables (in our case 15 out of the 36 variables were selected for each perturbed tree). In RF, a very large number of trees (500–2,000) are grown (hence a 'forest' of trees) and averaged to yield powerful predictions closer to the true error of the estimated population rather than just the training error.

The outputs of the RF can then be compared and evaluated using a set of map comparison tools. We used the Pearson's correlation, the Kappa statistic, and the fuzzy Kappa (Hagen, 2003) to compare actual FIA to modeled current prediction. These tools are described fully in Prasad *et al.* (in press). RF also provides output on the relative importance of each variable in the model. In addition, the stability of the model can be evaluated with the BT output by noting the variability of the deviance across 50 trees. With a stable model, the deviance explained would not vary much across trees, while an unstable model would yield trees explaining varying degrees of deviance. Finally, the relationship among variables, the geographic location of predictors, and the scale of influence can be assessed with RTA outputs.

2.2 SHIFT

SHIFT is a model to assess colonization probability during 100 years of warming climate; details on the model are given in Iverson *et al.* (1999b, 2004c). Following DISTRIB, further data preparation is needed prior to running SHIFT, including a smoothing of the IV values within a boundary established by a digitized (Prasad and Iverson, 2003) representa-

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

Climate

AVGT	Mean annual temperature (℃)
JANT	Mean January temperature (℃)
JULT	Mean July temperature (℃)
MAYSEPT	Mean May–September temperature (℃)
PPT	Annual precipitation (mm)

Elevation

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

ALFISOL	Alfisol (%)
ARIDISOL	Aridisol (%)
ENTISOL	Entisol (%)
HISTOSOL	Histosol (%)
INCEPTSOL	Inceptisol (%)
MOLLISOL	Mollisol (%)
SPODOSOL	Spodosol (%)
ULTISOL	Ultisol (%)
VERTISOL	Vertisol (%)

Soil property

BD	Soil bulk density (g/cm³)
CLAY	Percent clay (<0.002 mm size)
KFFACT	Soil erodibility factor, rock fragments 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 (m³ of timber/ha)
PERM	Soil permeability rate (cm/h)
PH	Soil pH
ROCKDEP	Depth to bedrock (cm)
ROCKFRAG	Percent weight of rock fragments 8–25 cm
SLOPE	Soil slope (%) of a soil component
TAWC	Total available water capacity (cm, to 152 cm)

Land use and fragmentation

AGRICULT	Cropland (%)
FOREST	Forest land (%)
FRAG	Fragmentation Index (Riitters *et al.*, 2002)
NONFOREST	Non-forest land (%)

tion of Little's (1971, 1977) range boundaries. A forest density map was used which depicted the percent forest within each 1 km² (from Zhu and Evans, 1994). Additionally, a test bed of 80% randomly placed forest was created for calibrating migration rates to 50 km/century (a relatively high Holocene rate of migration and one that has not been shown in paleoecological studies to vary widely among species; hence the same rate was used for all species). Finally, research was needed to determine the approximate time to reproductive maturity, and thus the number of generations per 100 years, which ranged from 3 for *Quercus falcata* var. *falcata* to 6 for *Pinus taeda*.

Next were the SHIFT model runs, using first the 80% random forest map to calibrate the migration rate to 50 km/century. Then, the obtained parameters were used to run SHIFT for a 100-year migration, using 50 replicates which each correspond to a 2% probability of colonization. The output result was a 1 km cell map which indicated the probability of colonization after 100 years of migration under a climate change equivalent to 100 km per century. These outputs could then be used to calculate areas of potentially colonized forest, calculated at the 2, 20, and 50% probability of colonization but reported only at 20% in this paper.

3. Results and Discussion

3.1 Climate change in eastern United States

The climate of the eastern United States is expected to change considerably according to several climate scenarios (National Assessment Synthesis Team, 2001). As shown in Table 3, the CCC scenario is a much warmer and drier scenario as compared to the Hadley scenario. For example, average January temperatures are expected to be over 6°C warmer by 2100 in the CCC scenario, but only about 1℃ warmer in the Hadley scenario.

Table 3. Area-weighted averages for several climate variables for the eastern United States.

Variable	Current	Hadley	CCC
Jan. temp, ℃	−1.7	−0.8	4.9
July temp, ℃	23.5	27.0	28.5
Ave. temp, ℃	11.6	14.3	17.2
May–Sept. temp, ℃	20.6	23.3	26.0
PPT, mm	1,043	1,285	1,083

Table 4. Correlation and Kappa scores for RTA, BT, and RF among four tree species.

	Correlation			Kappa			Fuzzy Kappa		
	RTA	BT	RF	RTA	BT	RF	RTA	BT	RF
Picea rubens	0.864	0.945	0.953	0.576	0.586	0.589	0.660	0.659	0.660
Pinus banksiana	0.734	0.896	0.919	0.430	0.447	0.477	0.497	0.517	0.539
Fraxinus americana	0.693	0.907	0.923	0.357	0.417	0.441	0.375	0.443	0.455
Quercus montana	0.795	0.940	0.947	0.506	0.513	0.532	0.567	0.579	0.590

3.2 Evaluation of statistical tools

Table 4 shows the correlation and Kappa statistics for four species using RTA, BT, and RF: in each case RF has the superior result, although BT is very close. An evaluation of all four statistical procedures used to predict potential suitable habitat via the DISTRIB model shows some advantages and disadvantages of each method: RTA is the easiest to interpret but, with MARS, is also less accurate. MARS does fine on current vegetation modeling but fails on future predictions (Prasad *et al.*, in press). BT and RF both utilize multiple regression trees which increase accuracy, though interpretation is more difficult. BT and RF were clearly superior in reproducing actual importance value distributions, and also in producing more appropriate representations of future suitable habitat following climate change. We favor RF over BT because it creates a smooth output in a logical gradient fashion. A combination of RTA, BT, and RF may yield the best and most interpretable maps of suitable habitat. The superior prediction capability of RF is best used to map future scenarios, while RTA and to some extent BT can be used for their interpretive abilities. If the individual trees (among BT) are similar, a single RTA tree can be used to map what predictors are driving the distribution of the species spatially; a very unique aspect of RTA that offers additional insights into the species distribution (Iverson and Prasad, 1998; Iverson *et al.*, 1999a).

3.3 DISTRIB—estimates of suitable habitat

RF outputs yielded estimates of area coverage for each of 135 species, as modeled for the current time, and for year 2100 according to the Hadley and CCC global circulation model scenarios (Table 5). According to this assessment using the Hadley scenario, 34 species are inclined to have a reduced habitat (by at least 10%), and 87 species will have an increased habitat in the eastern United States by year 2100 (Table 6). For the CCC scenario, 52 species would have decreased habitat and 66 species would have increased habitat. Note, however, that 73 of the 135 species bound Canada, and as such a full assessment of the potential change in suitable habitat is not possible, as only the habitat contained within the United States was analyzed. Work with Canadian colleagues to better assess the potential habitat changes within Canada is ongoing. Our data show that, of the decreasing species, most bound Canada (Table 6). On the other hand, most of the increasing species are more southern in nature that do not yet reach the Canadian boundary. In both cases, it is simply the northward shifting of habitat that is responsible for these patterns.

3.4 DISTRIB/SHIFT—estimates of migration into suitable habitat

The SHIFT model was used with five representative species (that did not have suitable habitat bounding Canada and which had a range of importance values, e.g., very low in *Diospyros virginiana* to very high in *Pinus taeda*) to estimate migration under climate change forcing (equivalent to migration rates during the Holocene of about 50 km/century). The SHIFT model considers the fragmented nature of the habitat, the abundance of the dispersing species, and the time it takes the tree species to become mature within the 100-year period.

Following the DISTRIB estimates of future suitable habitat, it is next appropriate to evaluate the proportion of suitable habitat that may become colonized during the next 100 years; this result is possible by intersecting output maps from both DISTRIB and SHIFT (Table 7).

It is clear from Table 7 that only a small proportion of the new suitable habitat is likely to be colonized in the next 100 years. Only about 5% or less of the new habitat, for any of the five test species, has at least a 20% probability of being colonized during that period. Therefore, there is a serious lag between the potential movement of suitable habitat and the potential for the species to migrate into the new habitat. However, humans could either accidentally

Table 5. Current (modeled) and potential future habitat area resulting from two scenarios of climate change in the eastern United States. An asterisk indicates the species bounds Canada so that a full range assessment was not possible.

Species	Current	Hadley (km²×1,000)	CCC
Abies balsamea*	390	216	165
Chamaecyparis thyoides	18	30	7
Juniperus virginiana*	1,239	2,453	2,842
Larix laricina*	274	186	148
Picea glauca*	228	73	14
Picea mariana*	254	43	11
Picea rubens*	179	159	139
Pinus banksiana*	258	175	76
Pinus clausa	78	326	543
Pinus echinata	887	1,534	1,958
Pinus elliottii	452	1,013	1,382
Pinus glabra	18	48	12
Pinus palustris	466	1,069	1,133
Pinus pungens	9	16	23
Pinus resinosa*	394	337	227
Pinus rigida*	114	107	99
Pinus serotina	138	168	203
Pinus strobus*	884	789	610
Pinus taeda	1,198	1,963	2,162
Pinus virginiana	525	667	654
Taxodium distichum	339	505	427
Taxodium distichum (var. nutans)	180	520	1,186
Thuja occidentalis*	380	242	182
Tsuga canadensis*	561	489	378
Acer barbatum	5	10	11
Acer negundo*	1,381	1,478	1,182
Acer nigrum*	16	11	5
Acer pensylvanicum*	302	199	99
Acer rubrum*	2,513	2,688	2,560
Acer saccharinum*	825	1,088	850
Acer saccharum*	1,693	1,627	943
Acer spicatum*	54	14	1
Aesculus glabra	65	57	32
Aesculus octandra	6	10	9
Amelanchier sp.*	261	214	171
Asimina triloba*	52	100	35
Betula alleghaniensis*	459	324	173
Betula lenta*	320	335	344
Betula nigra	77	134	65
Betula papyrifera*	545	346	56
Betula populifolia*	116	87	48
Bumelia lanuginosa	1	4	3
Carpinus caroliniana*	1,019	1,367	1,476
Carya aquatica	128	158	108
Carya cordiformis*	616	928	685
Carya glabra*	536	940	768
Carya illinoensis	108	440	446
Carya laciniosa*	13	17	8
Carya ovata*	895	1,166	896
Carya texana	270	872	1,504

Species	Current	Hadley (km²×1,000)	CCC
Carya tomentosa*	550	976	1,141
Castanea dentata*	4	12	10
Catalpa speciosa	47	46	69
Celtis laevigata	369	1,075	1,376
Celtis occidentalis*	1,044	1,340	1,215
Cercis canadensis	410	586	668
Cornus florida*	1,554	1,986	2,105
Diospyros virginiana	621	1,490	1,697
Fagus grandifolia*	1,230	1,228	866
Fraxinus americana*	1,608	1,934	1,694
Fraxinus nigra*	468	294	207
Fraxinus pennsylvanica*	1,822	2,126	2,074
Fraxinus quadrangulata*	6	8	7
Gleditsia aquatica	7	14	15
Gleditsia triacanthos*	622	1,021	1,090
Gordonia lasianthus	98	127	122
Gymnocladus dioicus	35	43	34
Halesia carolina	10	10	8
Ilex opaca	295	298	354
Juglans cinerea*	35	8	2
Juglans nigra*	1,050	1,288	1,054
Liquidambar styraciflua	1,314	2,231	2,148
Liriodendron tulipifera*	1,211	1,764	1,433
Maclura pomifera	529	986	997
Magnolia acuminata*	46	41	20
Magnolia grandiflora	27	103	43
Magnolia virginiana	418	736	635
Magnolia macrophylla	4	4	0
Morus rubra*	506	798	841
Nyssa aquatica	197	235	114
Nyssa ogeche	8	12	13
Nyssa sylvatica*	1,406	1,880	1,980
Nyssa biflora	391	539	532
Ostrya virginiana*	1,478	1,898	1,722
Oxydendrum arboreum	534	636	342
Persea borbonia	175	272	259
Platanus occidentalis*	561	902	660
Populus balsamifera*	198	38	27
Populus deltoides*	875	1,098	884
Populus grandidentata*	583	410	108
Populus tremuloides*	827	489	227
Prunus pensylvanica*	58	38	6
Prunus serotina*	2,262	2,527	2,073
Prunus virginiana*	109	41	10
Prunus americana*	25	18	23
Quercus alba*	2,270	2,617	2,488
Quercus bicolor*	108	103	41
Quercus coccinea	726	542	462
Quercus durandii	1	0	0
Quercus ellipsoidalis*	129	80	15
Quercus falcata (var. falcata)	1,043	1,695	1,906
Quercus falcata (var. pagodaefolia)	311	391	351
Quercus ilicifolia	18	21	18
Quercus imbricaria	196	304	140
Quercus laevis	145	312	246

Species	Current	Hadley (km² × 1,000)	CCC
Quercus laurifolia	489	850	1,166
Quercus lyrata	182	179	160
*Quercus macrocarpa**	911	940	832
Quercus marilandica	350	1,146	1,787
Quercus michauxii	45	24	11
*Quercus muehlenbergii**	313	536	405
Quercus nigra	952	1,549	2,114
Quercus nuttallii	86	91	87
*Quercus palustris**	246	376	206
Quercus phellos	547	702	668
*Quercus prinus**	654	848	805
*Quercus rubra**	1,988	1,966	1,536
Quercus shumardii	10	31	37
Quercus stellata	1,318	2,263	2,806
*Quercus velutina**	1,641	1,998	1,800
Quercus virginiana	184	552	1,146
Quercus incana	53	193	131
Robinia psuedoacacia	623	1,056	1,220
*Salix amygdaloides**	23	4	25
*Salix nigra**	614	863	632
*Sassafras albidum**	912	1,374	1,278
*Sorbus americana**	2	0	0
*Tilia americana**	995	887	434
Tilia heterophylla	0	1	1
Ulmus alata	777	1,947	2,316
*Ulmus americana**	2,081	2,289	2,282
Ulmus crassifolia	65	114	396
*Ulmus rubra**	1,245	1,534	1,188
*Ulmus thomasii**	26	78	6
Planera aquatica	46	55	48

Table 6. Comparison of future areal estimates for trees that are increasing, decreasing, or staying the same that are bound and not bound by Canada for two different climate scenarios. A tree species is increasing or decreasing if areal estimates are 10 % higher or lower than present estimates.

	Hadley	CCC
All species		
Decreasing	34	52
Increasing	87	66
Same	14	17
Species bounding Canada		
Decreasing	30	38
Increasing	34	22
Same	9	13
Species not bounding Canada		
Decreasing	4	14
Increasing	53	44
Same	5	4

or purposely move propagules into the new suitable habitat for certain species to mitigate some of these time lags.

4. Conclusions

We have demonstrated a methodology aimed at estimating the potential changes in tree suitable habitat following two scenarios of climate change in the current century. Conditions for tree growth are changing, and will continue to change as the planet's climate changes over the next 100 years. These changes can follow one of several different paths, depending on which scenario is used in the analysis. The two widely used general climate scenarios reported here, Hadley and Canadian Climate Center, have widely diverging climate paths, but both result in substantial changes in suitable habitat for most species. Overall, more species will have increasing habitat than decreasing habitat, especially with the Hadley scenario, under this analysis.

Changes in suitability for growing trees are only half the issue, however. Also critical is whether the species will be able to migrate into the new suitable habitat. With SHIFT, we also estimate, for five species, the potential for the new suitable habitat to be colonized within that 100 year period. Our analysis shows a very large migration lag in that only a small fraction of the new suitable habitat will likely be colonized. If these analyses prove to be true, the result would be a decrease in fit between species and environment so that the species in question would be more susceptible to various stress conditions and perhaps relegated to refugia where conditions are still satisfactory for the species.

The overall results are not unlike what others have obtained using other techniques, such as simulation (e.g., GAP) models or other forms of envelope models: tree compositions will change. How this change proceeds to create new forest communities under climate change depends in part on the opposing forces of the general longevity of trees relative to their mostly slow dispersal capabilities.

Table 7. Area of potential new habitat for Hadley and CCC (under DISTRIB), and the potentially colonized area (and percentage) of new habitat, at the 20% probability level (under SHIFT, intersected with DISTRIB).

Species	Potential new habitat		Potential colonized (20%)		Percentage (%)	
	Had	CCC	Had	CCC	Had	CCC
Quercus falcata var. *falcata*	603	1,339	24.9	26.4	4.1	2.0
Oxydendrum arboreum	543	542	11.9	13.0	2.2	2.4
Liquidambar styraciflua	196	687	10.0	15.4	5.1	2.2
Diospyros virginiana	304	792	3.9	6.5	1.3	0.8
Pinus taeda	218	822	7.0	11.9	3.2	1.5

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