Potential changes in habitat suitability under climate change: Lessons learned from 15 years of species modelling

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Climate change is being implicated in changes in forest structure and function--from species range shifts to increased forest mortality to changes in phenology. Based on historical patterns, the potential for change and even the direction of change will likely be species specific and significant. We take an empirical-statistical modeling approach using species abundance data from well recognized national inventories. For the past 15 years, we have developed and refined abundance-based habitat models utilizing the latest statistical techniques and have generated tools and summaries to explore potential changes of tree species habitats in the eastern U.S. (www.nrs.fs.fed.us/atlas). The DISTRIB model uses a statistically robust, predictive data-mining tool, RandomForest, to predict and map the potential habitat changes for 134 tree species and 147 bird species in the eastern United States. Each species is modeled individually to show current and potential future habitats according to two emission scenarios and three climate models. We produce lists of species that have a tendency to increase, decrease, or stay the same for any region. Because we model potential suitable habitats of species, our results should not be interpreted as actual changes in distribution of the species. Nonetheless, our models predict climate change will have large impacts on suitable habitat for many tree species, especially under a high carbon emissions trajectory. To help interpret and supplement the DISTRIB outputs for trees, we assigned modification factors for potential issues that cannot be specifically assessed with the DISTRIB model. We also use a spatially explicit cellular model, SHIFT, to calculate colonization potentials for some species, based on the abundance of the species, the distances between occupied and unoccupied cells and the fragmented nature of the landscape. By combining results from the three efforts, we aim to prepare estimates of potential climate change impacts for forest managers that can be used to aid in management decisions under climate change. Here we emphasize some of the lessons that we've learned in hopes that they may be helpful to others.

Keywords: climate change; eastern United States; RandomForest statistical modeling; trees

Introduction

Anthropogenic climate change is occurring. Even if greenhouse gas emissions were to stop today, the climate would continue to warm for the next 100 years (IPCC 2007). As the planet warms and the hydrological cycle becomes more vigorous, we are likely to encounter, among many documented trends, continued ecosystem changes including species shifts. Though much uncertainty remains in these predictions, convergence of paleoecological evidence (e.g., DeHayes *et al*., 2000) and modeling (Kirilenko *et al*., 2000) suggests that individual tree species will eventually undergo independent, and often radical, changes in distribution (Davis 1981, Webb and Bartlein 1992).Thus we support the modeling of individual species for assessing potential habitat changes with climate change, with the recognition that a thorough evaluation of species interactions is not possible with this approach.

Species-based approaches to modeling climate-driven changes in habitat thus far have relied primarily on empirically based statistical models using equilibrium-climate conditions (e.g., McKenney *et*

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al. 2007) and presence/absence data. A mechanistic, process-driven approach for modeling more than a few individual species would be too complex and would suffer from weak parameterization owing to lack of species-specific data.

Since 1994, our group has been using a statistical approach to project potential habitat changes for the trees of the eastern United States, using the U.S. Forest Service's Forest Inventory and Analysis (FIA) and soils data (Iverson *et al*. 1996). We have continuously revised our data, approach, and techniques, taking advantage of new and updated data, new climate models and emission scenarios, new robust statistical data mining and prediction approaches, new developments from other scientists, and progress in our own thinking (e.g., Iverson and Prasad 1998, 2001, 2002, Iverson *et al*. 1999, 2004, 2005, 2008a, 2008b, Prasad *et al*. 2006). The culmination of this effort for 134 tree species is contained within our tree and bird atlas web sites (see web citations below).

In this paper, we aim to capture some of the lessons we have learned from modeling species under various scenarios of climate change. It is not intended as a synthesis of modeling approaches or a biased endorsement of our own work. Instead our objective is to present one thread of scientific inquiry in which we have tried to overcome challenges and learn from our mistakes. Though we have conducted this work on only one small section of the globe, we believe that many of the lessons learned will be applicable elsewhere, and we hope, helpful for other investigators.

Materials and Methods

Our methods have been well documented (see references) and will not be reproduced in detail here. Rather we give our overall approach to the modeling via a flowchart (Fig. 1). First, the acquisition of quality data is paramount. We recognize that data for the eastern United States may be more complete than for many other regions of the globe but it is important to strive for the best data possible. We then use the DISTRIB model, a series of robust statistical models, to build and assess the reliability of each species model (Iverson *et al*. 2008a, 2008b, Prasad *et al*. 2006). These outputs, for 134 tree and 147 bird species, have been placed on-line (www.nrs.fs.fed.us/atlas). The SHIFT model is then used in conjunction with DISTRIB outputs for trees to stochastically model the possible colonization of the new suitable habitat within 100 years (Iverson *et al*. 1999, Iverson *et al*. 2004). Finally, we use modifying factors in an attempt to increase model usefulness by incorporating published species attributes to inform how the species is likely to respond under new climatic and disturbance regimes. The overall intention is to provide the best information possible, under the uncertainty limitations imposed, for decision-makers to work with in the face of climate change.

Results and Discussion

Summary of model outputs

The outputs of the models have been used for many assessments, ranging from national to regional (e.g., U.S. National Assessment (National Assessment Synthesis Team 2000); Northeast Assessment (Frumhoff et al 2007); Pennsylvania Assessment (Union of Concerned Scientists 2008); Chicago Assessment (Wuebbles et al 2008)). With a 20x20 km cell size, the outputs are intended to provide a relatively coarse, regional analysis of possible future trends to give citizens, researchers, and decision-makers. Though we have summarized and published results in a number of outlets (see references), the on-line atlases remain the best source for up-to-date information on each species.

Tree Atlas. The first version of the on-line Tree Atlas, launched in 1999 (Prasad *et al*. 1999) and published in hard copy (Iverson *et al*. 1999a), provides distributional maps, statistical reports, and life history information for 80 species of the eastern U.S. modeled under six climate models and 33 predictor variables (www.fs.fed.us/ne/delaware/atlas). Analyses and projections were performed at the county level (~3300 counties) in this version. The current Tree Atlas (www.fs.fed.us/atlas/tree_atlas) includes 134 species and utilizes updated climate models and 38 predictor variables analyzed over a 20x20 km grid (~10,000 cells). Distributional maps, statistical reports, and life history similar to the earlier atlas along with maps of Geographic Predictors, Hot-Spots, Niches, and Ranges are offered. New information includes maps, tables, and a box-plot analysis for each predictor variable, projections for forest types as deduced via a rule-based method to combine species, and summaries of potential species changes in state and regional assessments. Keyhole Markup Language (kml) files are available to download for viewing in Google™ Earth.

Bird Atlas. The first bird atlas, published in 2004 (Matthews et al 2004), modeled 150 species at the county level with 80 trees species as part of the predictors. The current atlas (www.fs.fed.us/atlas/birds) was produced in a similar fashion to that of the trees. It uses Breeding Bird Survey (BBS) data with climate, elevation, and vegetation (88 tree species) predictors to build models for 147 species of the eastern United States. The bird atlas produces much of the same research products as the tree atlas and allows the user to explore the bird results in light of the tree species work. It provides statistical summaries of the species model and the geographic predictors to identify potential climate and vegetation variables most associated with a given bird species (see also Rodenhouse *et al.* 2008).

Independent Data Support. Studies conducted by Woodall *et al.* (2009) that supports many of the tree models we have produced. They used a comparison of the biomass of larger trees (>2.5 cm diameter breast height) relative to density of seedlings (<2.5 cm diameter) across each species' range of latitude to help detect possible future trends in distribution. For most of the species, higher regeneration success was evident at the northern edge of their ranges. Of the 40 species they tested, all but 3 showed trends that agreed with projections of our models.

Lessons learned

In this section, we highlight some of the features of our modeling approach and the development of tools to make results useful for managers. We hope these 'lessons learned' will prove useful to others involved in similar efforts.

Always remember: "All models are wrong, some are useful". This famous quote, attributed to George Box (Box and Draper 1987), points out that models are just approximate conceptions of reality, and this fact must be clearly stated when presenting model outputs. Species models like ours only present possible trends in suitable habitat, and what really happens to species distributions depend on many other factors as well.

Use an ensemble of machine-learning, data-driven modeling tools. We used a statistical-empirical approach with decision-tree ensembles to model the effects of climate, soil, elevation, and landscape predictors on the abundances of the tree species and to predict changes in the distribution of potential habitats for future climates (Prasad *et al.* 2006, Iverson *et al.* 2008b). Because our data were nonlinear and nonparametric with numerous hidden interactions, they violated most statistical assumptions, and traditional parametric statistical approaches would have poorly captured these complex patterns. Therefore, newer machine-learning, data-driven approaches using decision-tree ensembles were used to predict and provide valuable insights into the important predictors influencing species distributions. Specifically we used a 'tri-model' approach: RandomForest (numerous decision trees with resampled data and randomized subset of predictors) for prediction, bagging trees (averaging of 30 decision-trees with resampling) for assessing the stability among individual decision-trees and a single decision tree to interpret the results if the stability among trees proved satisfactory (Prasad *et al.* 2006).

Use abundance-based information for model building. We used the FIA and BBS data to model relative abundances, unlike limited presence/absence information obtained from traditional sources like herbaria or county-based records. We could therefore use powerful regression-based approaches instead of the more common binary/classification approaches for modeling species distributions. The key advantage is that we can make analyses and interpretations based on the core of the species' ranges, rather than the more uncertain range boundaries that are equally weighted in presence/absence data. This distinction is crucial when it comes to modeling habitat responses to climate change. When there is considerable variability around projected changes in climate, a continuous response variable allows the model to focus on core areas of a species distribution where there is greater certainty of species occurrence. An example of the value of using abundance based models can be quantified using sugar maple. When modeled as presence/absence, the change in habitat for one climate model is a 90% loss in the extent of the species habitat, but when run with abundance, the loss is only 36% of its current habitat range. The difference can be attributed to the binary presence/absence and the lack of abundance values distinguishing core from the edge of the species range.

Use non-climatic variables in combination with climatic variables for stronger models. We have found that the use of relevant non-climatic variables, in addition to the climatic ones, is an advantage. The soil, elevation and landscape predictors enabled the decision-tree to select non-climatic predictors that often contribute to the prediction-strength of a species' model. Even though the inclusion of non-climatic variables may contribute to collinearity and cause some confusion in the choice of the selected variables, we noticed that the benefits out-weighed the drawbacks. For example, we were able to delineate species not primarily driven by climate in addition to increasing the prediction accuracy. In fact, even though there was no dearth of observations in our dataset, one of the strengths of RandomForest is the ability to handle large number of predictor variables for datasets with limited observations without overfitting (Cutler *et al.* 2007).

Couple vegetation model outputs with bird models to enhance bird model outputs. We have found that coupling models of trees and birds provides further evidence to the importance of non-climate variables in species models. As with the models of tree species, the bird models benefit greatly by using non-climate variables as potential predictors. The role of climate conditions in shaping broad patterns of bird distributions and diversity (Currie 1991) have long been established, and if data are only available at the level of presence/absence, modeling climate conditions alone can capture the range of a species (Thuiller *et al.* 2004). However, the occurrence of birds on the landscape is further determined by specific habitat requirements and when modeling species distribution patterns, it is important to consider the landscape features contained within a climate space. Our models of 147 bird species contain climate, elevation, and tree species importance values as potential predictors. The importance of vegetation characteristics can be linked to specific habitat requirements of bird species and these features play an important role in the hierarchical nature of habitat use by bird species (Fearer *et al.* 2007). Traditionally, we would have used vegetation classes such as forest types to model contemporary bird distributions. However, because tree species respond individualistically to climate change, we cannot assume that contemporary forest types will remain intact. By using the individual tree species as predictors, we can consider the potential future habitat in terms of changing climate and vegetation. In the end, our models show a high reliance on the tree species variables (mean of 4 tree variables in the top ten most important variables per bird species model). When tree information is not included, 50 - 60% of the bird species models show the potential for greater change (either more losses or more gains) in habitat.

Give some assessment of the reliability of each model. Some species are more reliably modeled than others. For example, species with highly restricted ranges with low sample size often produce less satisfactory models as compared to more common species (Schwartz *et al.* 2006). There are therefore quite large differences in the reliability of the predictions among species. The tri-model approach gave us the ability to assess the reliability of the model predictions for each species, which was classified as high, medium or low depending on the assessment of the stability of the bagged trees and the R^2 in RandomForest. If the model reliability of a species was high, we could use a single decision-tree to map the important predictors influencing the distribution geographically. This high rating occurred for 55 of 134 tree and 59 of 147 bird species in our models. Even if the model reliability was medium or low, RandomForest predicts better without overfitting due to its inherent strengths compared to a single decision-tree (Cutler *et al.* 2007).

Combine species into potential community types to provide valuable summaries of overall tendencies. In the United States, the Forest Service uses 26 forest types to represent the general composition of the nation's forests. These forest types are generally recognized by the informed public and policy makers. Through the use of rule-based measures to combine species importance values, we have prepared maps of potential changes in suitable habitat for 10 forest types that occur in the eastern U.S. (Fig. 2, Iverson and Prasad 2001). These outputs, in a single set of figures, reveal potential loss of the spruce-fir and aspen-birch types and gains in oak-hickory and southern pine types. Such information would be difficult to portray with single species maps.

Separate the discussion of potential changes in suitable habitat from that of potential species range changes. It is important to clearly separate the discussion of where the habitat suitability may potentially change for a particular species from where the species may actually occur by a certain time. Obviously for trees, there will be large time lags, dispersal and establishment limitations, and refugia which will dictate the rate of migration into the new suitable habitat as projected by DISTRIB.

To elucidate the difference between habitat and species movements, we developed a cell-based model, SHIFT, to simulate migration of selected tree species over a 100 year period (Schwartz *et al.* 2001; Iverson *et al.* 2004). 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. Among five species, less that 15% of the newly suitable habitat was modeled to be potentially colonized within 100 years (Iverson *et al.* 2004).

Consider variations in disturbance, biology, and model issues on each modeled species. No model, statistical or otherwise, can include all the biological or disturbance factors that may influence a species' response to climate change. We addressed some of the uncertainty among the models related to 9 biological and 12 disturbance modification factors (ModFactors) that influence species' distribution. These factors can modify the results of the models by increasing or reducing the potential future importance of a species. Each species is given a score based on the literature, and can be changed by managers as they consider local conditions for each of the factors. With knowledge of site-specific processes, managers may be better suited to interpret the models after ModFactors have been considered.

While not yet available for release, an interactive spreadsheet has been developed for each tree species. Default values related to the general distribution of the species provide baseline information in which users are encouraged to modify based on local knowledge and site conditions. The ModFactor values can then be used to modify the interpretation of the importance values of the models. The goal of this effort is to provide information on the distribution of species under climate change that accounts for the natural processes that influence the final distribution. In addition, this approach encourages decision-makers to be actively involved in managing tree habitats under projected future climatic conditions.

Clearly articulate the weaknesses and strengths of the approach. It is important to identify weaknesses and strengths as these must be evaluated when comparing among approaches and when applying results to management policies. Important weaknesses to our modeling approach include:

1. The DISTRIB models are limited in scope to modeling the potential current/future suitable habitats – not their actual future distributions, although SHIFT begins to address this issue.
2. The FIA and BBS data are spatially sparse so that fine-scale analyses are not usually appropriate – 20 x 20 km is about right.
3. The data-driven methods depend on a decent sample size (>~50 cells), and models for rare species are likely to have limited inference.
4. The methods assume the species are in equilibrium with the environment, so that they are inappropriate for species known to have rapidly changing distributions (e.g., invasives).
5. There likely are better environmental predictors that could be used
6. Not all species have their entire ranges captured with abundance data, so that some artificial boundary limits will be imposed.
7. The models do not account for many biological attributes (e.g., competition) and disturbance factors that affect species' abundance, although we are attempting to account for these to some extent with the ModFactors.

Important strengths of our modeling approach, many of which are incorporated into other lessons learned, include:

1. FIA data are extensive, statistically sound, and non-biased.
2. The use of 31 non-climate variables to model tree species abundance helps capture possible 'barriers' or 'facilitators' to species' movement.
3. The analysis and prediction are based on the species' core of distribution via abundances; using the range edges via presence/absence maps are more susceptible to error.
4. We use extremely robust non-parametric statistical tools using an ensemble "tri-model" approach. RandomForest is surfacing in many studies as a superior modeling tool and is more stable compared to similar methods when predicting into novel environments.
5. By combining multiple plots within a 20x20 km cell, the models reduce local heterogeneity for more regional accuracy.
6. The reliability of individual species models can be evaluated.
7. The non-parametric, statistical models use different variables/parameters to describe primary drivers in different parts of its geographic setting. This is large advantage over multiple regression approaches that force variables to operate the same everywhere.

8. The statistical models account for reality in that a particular species exists where it is, in spite of all legacies over decades and centuries. It therefore integrates over historic disturbances and climatic phenomena.
9. The models are based on statistical inference and need not be parameterized with a large suite of variables that are imperfectly known or cannot be adequately generalized for a species throughout its range.
10. The models allow production of ranked lists of species that may be in greatest risk or likely to have sufficient suitable habitat for future management.

Conclusions

In this paper, we have attempted to relay some lessons learned over our 15-year history of modeling current and potential species distributions. We provide the following considerations (based on the strengths and weaknesses identified from our approach) for decision-makers to place these results in prospective as they face the difficult challenges to managing under climate change.

1. Regarding climate change predictions: plan for the most species habitat changes (high emissions) but work to encourage lower emissions.
2. It is likely that species distribution models produced before the explosion of machine-learning tools (e.g., RandomForest, ~2005) will be inferior to those produced later. Insist on robust predicting tools like RandomForest for species-level modeling.
3. Pay attention to the reliability of each species model – and even for high reliability models, there still will be errors and uncertainties!
4. Less common species are more prone to error. Rare species are especially difficult.
5. Edge boundaries are 'fuzzy', both now and in future –core areas of higher abundances are more indicative of potential species behavior under climate change.
6. Use species models as guidelines for regional trends – because of uncertainties, they are not usually appropriate for fine-scale management without the regional context.
7. Consider modifying factors (e.g., disturbance, biological) not included in the models as modifiers to model outputs.
8. Concentrate on the factors you can do something about (e.g., silvicultural options).
9. Encourage multiple modeling efforts, both statistical and process-based, so that where models agree, confidence is strengthened, and where they disagree, a closer look is warranted.

Species-distribution models, in the form presented here, can be used to:

1. Learn which species are present, or could occur, in your location now.
2. Learn which environmental factors are likely driving species' suitable habitat, e.g., which are most susceptible to climatic factors.
3. Learn which species are most and least likely to have their available habitats shifted in the future, and how much.
4. Learn which species could incur the most risk (e.g., local extinction) under climate change.
5. Learn which species could become newly suitable for your location (e.g., from warmer climates).
6. With outputs from a model like SHIFT, learn where potential colonization could occur within 100 years.
7. With modification factors, identify which factors are most likely to modify model outputs, whether they will increase or decrease the changes projected with the species modeling, and which factors you might be able to influence via management.

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Figures

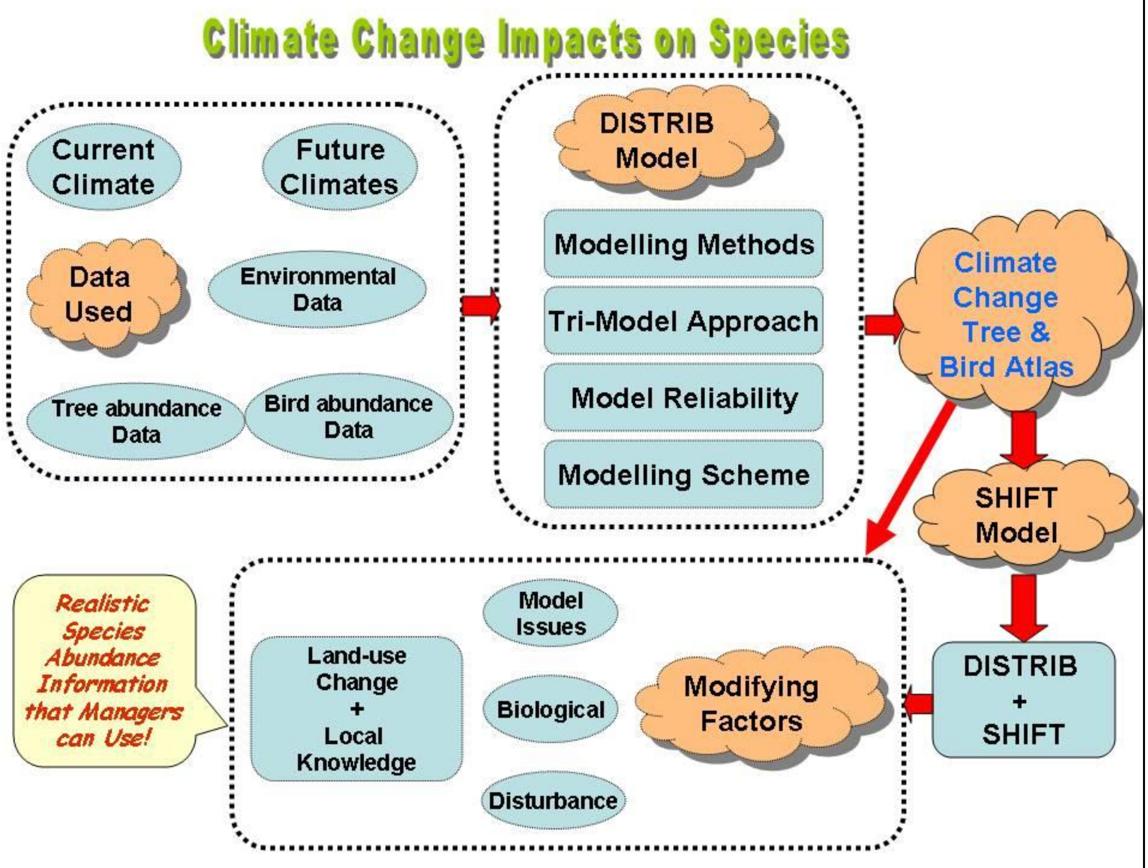
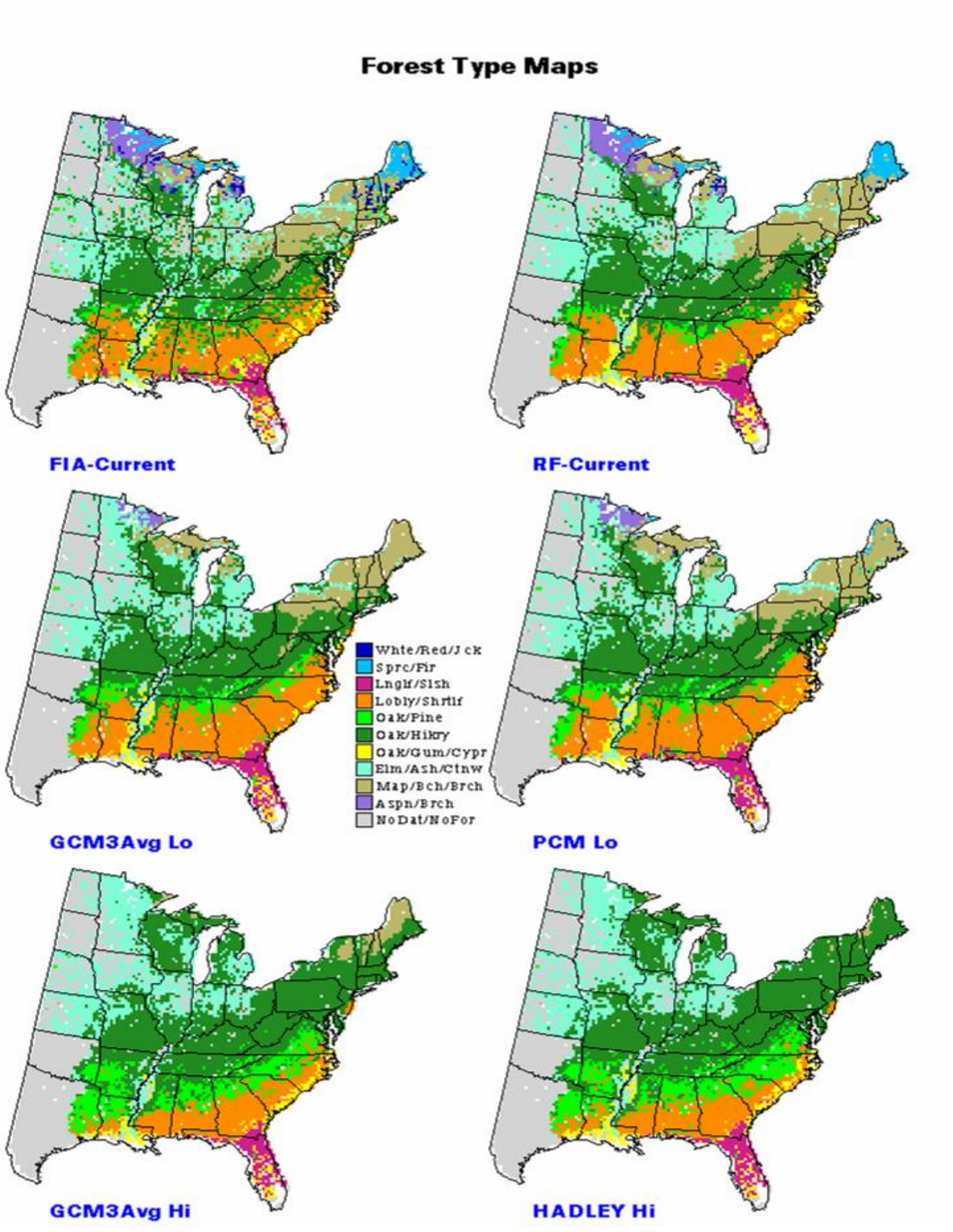


Figure 2. Potential changes in forest types under various scenarios of climate change for the eastern United States.



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