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MODELING BIRD SPECIES OCCURRENCE IN CURRENT AND FUTURE LANDSCAPES

By

Stephen Nicholas Matthews

B.S. Frostburg State University, 1997

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Wildlife Ecology)

The Graduate School

The University of Maine

May, 2003

Advisory Committee:

Raymond J. O'Connor, Professor of Wildlife Ecology, Advisor

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By Stephen Nicholas Matthews

Thesis Advisor: Dr. Raymond J. O'Connor

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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With mounting evidence that global temperatures have increased significantly over the last century and the projections of greater changes in climate by the end of this century, understanding the potential consequences of these changes for species is essential to conservation efforts. Here I evaluate the potential response of birds to projected climate change by using regression tree analysis to create models of species distributions under current conditions from Breeding Bird Survey data and then project these models onto General Circulation Model (GCM) scenarios of global climate change.

Before modeling species responses to climate change, I selected seventeen bird species to evaluate several considerations that could influence the ability to effectively model species distributions. First, I addressed the spatial resolution of the analysis. GCM data are readily available at a relatively coarse-grain compared to bird data. Since the spatial resolution of an analysis can greatly affect the outcome, I, therefore, assessed the consequences of modeling bird abundance at the 640-km^2 hexagonal grid (fine-grain) and the county resolution (coarse-grain) in the eastern United States. The results indicated that county resolution models produced good predictions of current bird distributions. Next, I compared two sets of climate data to ensure that the climate outputs from GCMs were as effective in modeling bird distributions as climate variables currently used in ecological studies. There were no differences of the overall model goodness of fit between the two sets of species models. The results from these analyses indicated that effective models of bird distributions at the county resolution could be constructed, provided both climate and land cover variables were present as predictors.

Following these evaluations I was able to model current abundance for 152 bird species. These models were projected onto two GCM scenarios. The projected response of birds under the two GCM scenarios varied greatly among species. Overall, both GCM scenarios projected approximately 49% of the species to decrease markedly and 22% to increase in their eastern United States populations. These results indicate the potential for large shifts in bird distributions in response to global climate change.

The heightened awareness of our Earth's increasing temperature has been linked to the rapid increase in greenhouse gases. Planting forests on marginal agricultural land has emerged as a promising proposal to sequester excess carbon dioxide, but none of these afforestation studies have considered the costs or benefits associated with impacts on wildlife. By combining information on current forest and farmland bird abundances with the results from simulations of carbon sequestration policies in South Carolina, Maine, and southern Wisconsin, it is possible to quantify the impacts of land use decisions on bird populations. I estimated losses respectively of 12.2 %, 10.8 %, and 11.7 % in farmland birds and gains of 2.5 %, 3.2 %, and 21.8 % in forest species in South Carolina, Maine, and southern Wisconsin. The results from this analysis reveal the importance of considering the effects of large-scale land use decisions on wildlife.

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INFLUENCE OF GRAIN SIZE ON BIRD DISTRIBUTION MODELS: SHIFTING FROM 640 KM^2 HEXAGONS TO COUNTIES

1.1 Abstract

The General Circulation Models (GCM) used to describe global climatic patterns are created at very coarse-grains. In contrast, very fine-grained studies typically dominate ecological studies, often over very restricted geographic areas. This inequality of scales is recognized (Root and Schneider 1993) and potentially leads to spurious modeling results. Therefore, I assessed the consequences of modeling bird species occurrences at two different grain sizes in the eastern United States. The extent of the study included the area east of the 100th meridian, and the grains that I compared were a 640 km^2 hexagonal grid and the US county boundaries. These grains constituted a fine degree of resolution for GCM data and a very coarse degree of resolution for modeling bird species occurrences, respectively.

Using regression trees, I created models of 17 bird species at the hexagonal and US County grains. The same climate, land cover, and landscape pattern variables were included as potential predictors of the species occurrences in both model types. The hexagon models had a mean total $R^2 = 69.1\%$, with climate and fine resolution land cover variables contributing on average 32.0 and 24.0 percentage points to this total R^2, respectively. The county-level models for the 17 species had a mean total R^2 of 77.1%. These county models were clearly dominated by climate variables which contributed on average 57.0 percentage points to the total R^2, with fine resolution land cover variables only accounting for 11.6 percentage points. Climate variables were therefore more

important in the county-level models. The within species difference in the total R^2 between county and hexagon models averaged 8.0 (SD = 8.9) percentage points, with the greatest increases (7-24 percentage points) occurring in the 8 species whose hexagon models explained less then 70% of the species variation. The increases in explanatory ability of the models for those 8 species were partly due to the degree of spatial autocorrelation in the species occurrences; there was a relationship between the hexagon model total R^2 and the estimate of the spatial autocorrelation range ($r_s = 0.561$, $r_{s0.05(2)14} = 0.538$, $P < 0.05$). Therefore, species models with lower total R^2 contained fine-grained interactions with the surrounding landscape at the hexagon level. When I increased the grain to counties, coarser-grained climate variables entered into the model. This indicates that the fine-grained variability in the species data was smoothed as the grain was increased. For species that showed broader autocorrelation patterns in their occurrence, the shift from hexagon to county resolution resulted in smaller differences among the total amount of the species variability explained. This analysis indicates that models of species distributions at the U.S. county resolution produce representative models of species abundance, and use of county-grained data is appropriate for predicting responses of bird species to climate change.

1.2 Introduction

Considerable attention has been directed towards assessing the impacts of projected global climate change on species distributions (Walther et al. 2002, Sorenson et al. 1998). One approach for understanding how species will be redistributed in response to climate change uses future climate scenarios projected by General Circulation Models (GCM) (Iverson and Prasad 1998, Root and Schneider 2002). These models represent climate processes across the earth (Baede et al. 2001) based on the current understanding of the complex global interactions of physical processes that influence climate (Gates 1993). Currently, the evolution of GCMs allows for confident predictions of climate patterns at coarse degrees of spatial resolution (Albritton et al. 2001). However, consistent simulation of climate at fine resolution continues to be difficult, due in part to fine-grained uncertainties (e.g., cloud cover) and variation (e.g., sharp elevation gradients) (Schneider 1993).

The forecasting of future species distributions requires an ability to model individual species under current conditions and at a spatial resolution that is appropriate for identifying climate based determinants of species distributions. To this end, several studies have addressed coarse-grain species distributions and have identified correlations between environmental variables and either patterns of species richness (Currie 1991, Asmole 1963, O'Connor et al. 1996, O'Connor et al. 1999) or individual species ranges (Root 1988a). The existence of these relationships provides an avenue to explore the responses of species distributions to climate changes projected by GCMs. However, modeling the occurrence of individual species across their range requires much data, which are often not available. Birds are a notable exception to this because of the availability of distributional data from annual Breeding Bird Surveys (BBS) in the conterminous United States since 1969 (Robbins et al. 1986).

Projections of bird species responses to climate change require modeling of current bird species occurrence at the coarse spatial resolution of GCM outputs and using environmental variables generated from GCMs. However, modeling bird species at the coarse-grain of GCMs can potentially mask important fine-grained habitat relationships and produce an unrepresentative model of the species distribution. Nevertheless, in appropriate circumstances models at coarse-grain can be expected to have higher predictability than their fine-grain counterparts (Maxwell and Costanza 1994), and the coarser resolution may highlight important long-wave influences of climate conditions on the species (Root 1988a).

Given the dichotomous effects resulting from the choice of grain size, I assessed the consequences of modeling bird species in the eastern United States at two spatial resolutions: a 640 km^2 grid, which has proven to be an appropriate resolution for predicting bird species richness (O'Connor et al. 1996), and US counties, which has been used for projecting potential future distribution of tree species under various GCM scenarios (Iverson and Prasad 1998). If current bird distribution can be successfully modeled at the county resolution it would be reasonable to extend the county-based approach of Iverson and Prasad (1998) to the modeling of potential future bird distributions under various GCM scenarios.

1.3 Methods

1.3.1 Spatial grain

The fine-grained analysis was based on the EMAP 640 km^2 hexagonal grid developed by White et al. (1992). This grid partitions the conterminous United States into approximately 12600 hexagons, and is fine enough to represent relatively small patches within continental landscapes. The hexagons are an appropriate basis for conducting analyses on BBS data, because the size of the hexagons matches well to the length of BBS routes (O'Connor et al 1996).

The course-grained analysis was based on US counties. A major disadvantage in using counties is the large variance in size that occurs in counties throughout the United States. However, the present analysis was confined to counties east of the 100th meridian where county size is smaller and more homogenous.

1.3.2 Bird data

Species occurrences were derived from Breeding Bird Survey (BBS) data from 1981-1990. Specifically, O'Connor et al. (1996) selected 1223 representative BBS routes and overlaid them with the 640 km ^{2} hexagonal grid of White et al. (1991) for the conterminous United States, and these data comprised the bases for the bird data in my analysis. For each of these hexagons an incidence value - the proportion of surveys on the corresponding BBS route in which the species was identified - was recorded. Given the typical proportional relationship between incidence and absolute abundance for most organisms (Hanksi 1992), these incidence values were interpreted as a measure of absolute abundance, but they are still not direct measures of abundance because the unique and unidentified slope linking incidence and abundance for each species is unknown.

Seventeen species were selected for the present analysis (Table 1.1). Because the goal was to examine the effects of modeling at county rather than hexagon resolution by presenting the modeling process with a cross-section of potential issues, the usual criterion of random selection could be relaxed. The selection was made primarily based on preliminary regression tree models for more than 300 species at the hexagon-resolution, using three criteria. First, in order to predict a species response to climate change it will be important that a model of its current distribution captures much of the

Table 1.1. List of the species included in this study.

Species
Eastern wood-pewee (*Contopus virens*)
Least flycatcher (*Empidonax minimus*)
Orchard oriole (*Icterus spurius*)
Baltimore oriole (*Icterus galbula*)
Field sparrow (*Spizella pusilla*)
Northern cardinal (*Cardinalis cardinalis*)
Rose-breasted grosbeak (*Pheucticus ludovicianus*)
Dickcissel (*Spiza americana*)
Summer tanager (*Piranga rubra*)
Magnolia warbler (*Dendroica magnolia*)
Black-throated green warbler (*Dendroica virens*)
Pine warbler (*Dendroica pinus*)
Prairie warbler (*Dendroica discolor*)
American redstart (*Setophaga ruticilla*)
Gray catbird (*Dumetella carolinensis*)
Brown thrasher (*Toxostoma rufum*)
Blue-gray gnatcatcher (*Polioptila caerulea*)

species variability across its range. Therefore, I only included models that explained more than 50% of the total species occurrence. Second, I selected species with distribution models that were largely explained by a climate and land cover variables, such that some species models were dominated by climate variables, some by land cover variables, and others had a balance of both. Finally, I selected species with ranges in the eastern United States (or with the core of their range in the east). Using this process, the seventeen species selected occupy habitats ranging from forest interior to open fields, and models that explained from 50-88 % of the species occurrence at the 640 km^2 resolution (Table 1.1).

Once the species were selected, I assessed the spatial autocorrelation of their distribution at the 640 km^2 hexagonal resolution. This exploratory analysis was necessary because the variability between close points is smoothed out as grain size is increased: species that show considerable variation in their abundance over small areas could therefore have large reductions in variability relative to species with broader, less variant distributions. For some species, this could result in disproportionate changes in model predictability as the grain size is increased. Prior characterization of spatial autocorrelation patterns for each species could then provide crucial information. To evaluate the spatial autocorrelation of each species, I used semivariograms with the robust estimation procedure of Cressie and Hawkins (1980) as provided in S-Plus version 6 (Insightful corporation 2001). The semivariogram describes the average variation between data points as a function of the distance between the data points (Chiles and Delfiner 1999).

1.3.3 Predictor variables

Several land cover, landscape pattern and climate variables were used as potential predictors of the bird species occurrence. All variables had previously been aggregated to the 640 km^2 grid of the conterminous United States (O'Connor et al. 1996). Available climate variables consisted of forty-year averages of annual precipitation (mm), January temperature (°C), July temperature (°C), and a seasonality index (difference of July and January temperature in °C) (O'Connor et al. 1996). For each of these metrics the long-term mean, maximum and minimum were used as potential predictors. The land cover variables were derived by Loveland et al. (1991) from advanced very high resolution radiometry (AVHRR) data at 1 km^2 resolution and classified into 159 land cover classes. The land cover classes were reported as a proportion of a given land cover class in each hexagon (i.e. if a land cover was present in 576 1-km^2 pixels the hexagon would receive a value of 0.9 (576/640)). O'Connor et al. (1996) added an urban class, bringing the total to 160 land cover classes. These detailed land cover classes were then aggregated to a coarser classification of 14 land cover classes by O'Connor et al. (1996) to approximate an Anderson et al. (1976) level II map of vegetation (e.g. deciduous forest, coastal wetlands). Both degrees of land cover resolution (14 classes, 160 classes) were included as potential predictors in this analysis because the optimum resolution of habitat attributes varies geographically over the eastern U.S. (J. Lawler et al. unpublished). Patch size characteristics were also compiled from the spatial patterning of these land cover classes in each hexagon. Other variables used were length of road, length of riparian systems, and elevation.

1.3.4 Cross-walking from hexagons to county resolution

In order to cross-walk (i.e., translate) variable values from hexagons to counties, a county boundary layer was overlaid onto the hexagonal grid. Then the polygons formed where hexagons and counties overlapped were identified. This process produced a list of unique polygon areas that contained the hexagon and county identification. The details of the cross-walk process varied for each type of data (e.g., bird distributions, climate maximums, road lengths).

For the bird species data, each polygon received its species incidence value from the hexagon it was associated with. Each species' incidence from the 1223 representative BBS routes had previously been spatially smoothed and interpolated to the 12600-hexagons in the conterminous United States (Yang et al. 1995). This allowed for complete coverage of the species incidence across their range, and matched the hexagon dataset of the independent variables. This polygon incidence was then area-weighted by its relative contribution to the county in which it was and the weighted county-level estimate was computed (Matthews et al. 2002).

This method was also applied for the various land cover estimates, as these too were proportions. In order to cross-walk the average patch size of each land cover variable, it was necessary to account for the number of 1 km^2 pixels in a polygon in addition to the area of the polygon. By finding both of these areas, the estimate of the county level average patch size was more accurate because it was weighted by the polygon area and the relative amount of a given land cover present in the county. The climate variables describing the long term averages for January temperature, July temperature, precipitation, and seasonality were cross-walked to a county-level estimate by area-weighting the proportion of the polygon in the county and then these weighted areas were summed to arrive at a county-level estimate

For maximum and minimum long-term climate data for January temperature, July temperature, precipitation, and seasonality, and scaled maximum patch size for each land cover class (the scaling of the maximum patch size variable was obtained by division by the national average patch size of that cover class, thus emphasizing for certain species the importance of the presence of small patches of rare land cover types), the polygons within each county that had the highest value for maximum and the lowest value for minimum variables were identified and tagged to the county. For data such as road and riparian length, the proportion of the polygon in each hexagon was identified. Then the metric was weighted by this proportion, assigned to the polygon, and summed across the polygons within the county to arrive at a county estimate.

Finally, there was a suite of variables that could not be readily cross-walked to county-level estimates. They included such variables as fractal dimension, and other scale-specific landscape pattern values. These variables were left out of the county resolution data frame of independent variables. These metrics occurred in five hexagon based models where they never contributed more than 4.1 percentage points to the total explanatory power of the model, so little information was lost to these omissions.

1.3.5 Statistical analysis

I evaluated the consequences of modeling the occurrences of 17 bird species at the hexagon and county resolution using regression tree analysis (S-Plus version 6, Insightful Corporation 2001). First, models were produced for each species at the 640-km^2 hexagon resolution (hereafter referred to as hexagon models) using the 1223 representative hexagons of O'Connor et al. (1996). Then models for the same species were produced at the county resolution (hereafter referred to as county models). Because the bird species data used to crosswalk the BBS data to the county resolution were the smoothed data of Yang et al. (1995), I also investigated whether the increased number of data points could have influenced the comparison between the hexagon and county species models. To do this, the spatially smoothed hexagon data of Yang et al. (1995) were used as response variables and the complete 12600 hexagon data set as predictor variables in regression tree analysis that otherwise proceeded as before. These models are hereafter referred to as complete coverage hexagon models.

I used regression trees (Breiman et al. 1984, Clark and Pregibon 1992) to construct models of bird species occurrences because they have several advantages over traditional regression methods. First, regression trees do not have strict assumptions of linearity, are less sensitive to outliers, and thus require no assumption of normality (Verbyla 1987). Secondly, the method's ability to handle interactions between independent variables by sub-setting the data in the tree building process eliminates the need to identify all possible interactions a priori (O'Connor et al. 1996, Iverson and Prasad 1998).

Regression trees recursively partition the response variable into ever-more homogenous groups defined by predictor variables. In the case of modeling a species distribution, as used in this analysis, the regression tree algorithm searched through the entire set of potential predictor variables and used each variable in turn to split the response variable into two groups. The binary split occurred at the threshold of the ordered independent variable value that best separated the sample into two groups. This

variable and threshold was adopted as the definitive split. The process was recursively conducted, thus repeatedly splitting the response variable subgroups until stopping criteria were reached. The resulting regression tree was then pruned back using ten-fold cross-validation (Breiman et al. 1984, Clark and Pregibon 1992). This procedure was necessary because original regression trees often represent over-fitted models.
After cross-validation, any of the variables in the regression tree that explained less then one percent of the species deviance was removed to eliminate a small residual bias towards large regression trees associated with the default cross-validation in S-Plus (J. Sifneos personal communication).

With the large number of variables included as possible predictors, it was necessary to examine each of the final variables in the species models to see if it was confounded, in space, with locally correlated variables. To accomplish this, each variable in the regression tree was perturbed in turn by five percent (i.e., the predictor variable was randomly perturbed such that each data point had an equal chance of being altered) and the model was re-run for each perturbation (Lawler and O'Connor in preparation). This procedure allowed me to identify variables that were collinear at each split. Once the final regression tree model was created, validated and assessed, I calculated the percentage of the deviance associated with each variable in the model and the percentage of the total deviance explained by the model (represented as $100*R^2$).

1.4 Results

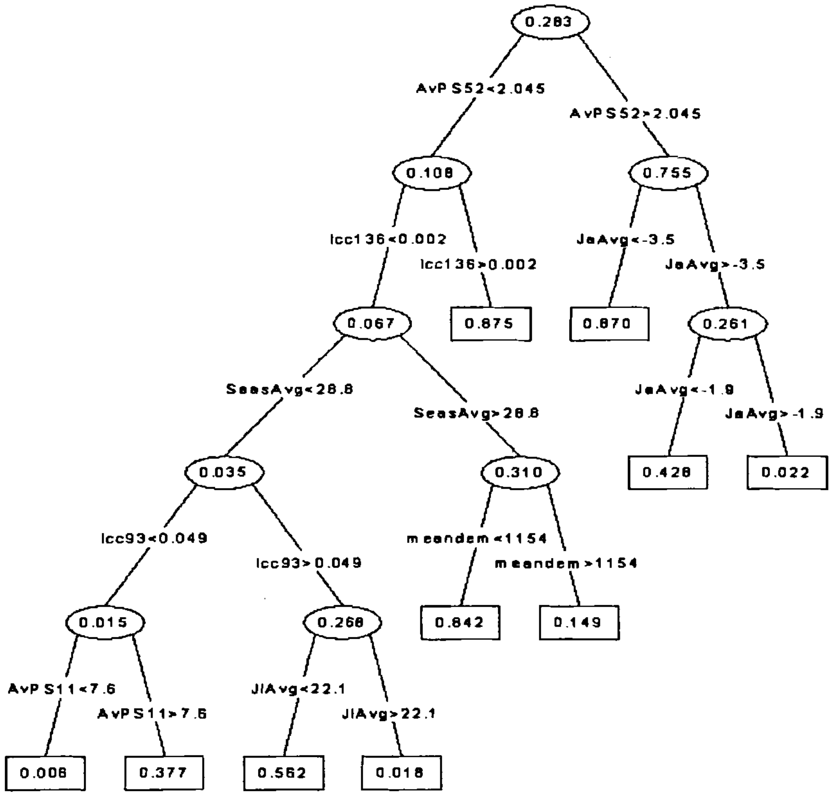
1.4.1 Species example

Before summarizing the results of the models for all species, I will provide an in-depth example using the rose-breasted grosbeak (*Pheucticus ludovicianus*) to illustrate the types of results obtained from the analysis. The hexagon model for the rose-breasted grosbeak used eight different variables to describe the species' occurrence in the United States (Figure 1.1a). The first split occurred at a threshold of the average patch size of Loveland et al.'s (1991) land cover class 52 (lcc52), i.e. cover dominated by forage, crops, hay and woodlots. The left subset contained areas with very small or no patches of land cover class 52, and the right subset encompassed the hexagons that had larger patches. The next split of the right branch occurred at the threshold of an average January temperature (JaAvg) of –3.5 C°. At this point the colder hexagons constituted a terminal node (no further predictors could be found) of the model, with an average grosbeak incidence of 0.870 (i.e., the species was recorded 87% of the time on the BBS routes in this region). The areas with average January temperature greater than –3.5 C°, the right hand side of this split, were partitioned again by average January temperature but at a warmer threshold (-1.9 C°). The sites with winter temperatures between –3.5 C° and –1.9 C° had average grosbeak incidence of 0.426, about half that of the sites below –3.5 C°; sites warmer than –1.9 C° were even sparser in grosbeaks, averaging 0.022 i.e. nearly complete absence. Moving back to the root node, we can apply the same method of interpretation to the left partition of the tree, where the daughter nodes of each partition were contingent on the nodes above. Figure 1.1a shows that 7 terminal nodes occurred on the left branch.

The rose-breasted grosbeak hexagon model involved five land cover variables, two climate variables, and one elevation variable. The relative importance of each of these variables is presented in Table 1.2. Average patch size of Loveland et al's (1991) land cover class 52 (crop/woodland dominated by forage, crops, hay and woodlots)

Figure 1.1. Regression tree structure from the rose-breasted grosbeak hexagon (A) and county (B) resolution models. The ellipses represent intermediate nodes in the regression tree, while the rectangles are the terminal nodes. For each internal node the regression tree shows the threshold split variable and value. The numbers in the ellipses and rectangles give the predicted bird species incidences at that point. AvPS52 is the average patch size of Loveland et al. (1991) land cover class 52 (land cover class of crop and woodland dominated by forage crops, hay, woodlots); AvPS11 is the average patch size of land cover class 11 (row crops dominated by corn and soybeans); JaAvg is average January temperature; JlAvg the average July temperature (°C); lcc9.lco2 is land cover class 9 of mixed (deciduous/coniferous) forests as measured in the Anderson level II coverage of O'Connor et al. (1996); lcc93 is Loveland et al.'s (1991) land cover class 93 of northern deciduous forest dominated by beech, birch, maple, oak, and pasture; lcc136 is land cover class 136 of northern mixed forest dominated by oak maple ash beech birch, jack pine and red pine; meandem is average elevation (m); max.elev is the maximum elevation (m); and ScMPS17 is the scaled maximum patch size of land cover class 17 of row crops dominated by corn and soybean (lcc17); SeasAvg is average seasonality (difference between July and January average temperatures (°C)).

A.


0.283
AvPS52<2.045
AvPS52>2.045
0.108
0.755
lcc136<0.002
lcc136>0.002
0.875
JaAvg<-3.5
JaAvg>-3.5
0.870
0.261
0.067
SeasAvg<28.8
SeasAvg>28.8
JaAvg<-1.9
JaAvg>-1.9
0.428
0.022
0.035
0.310
lcc93<0.049
lcc93>0.049
meandem<1154
meandem>1154
0.015
0.268
0.842
0.149
AvPS11<7.6
AvPS11>7.6
JlAvg<22.1
JlAvg>22.1
0.006
0.377
0.562
0.018

B.

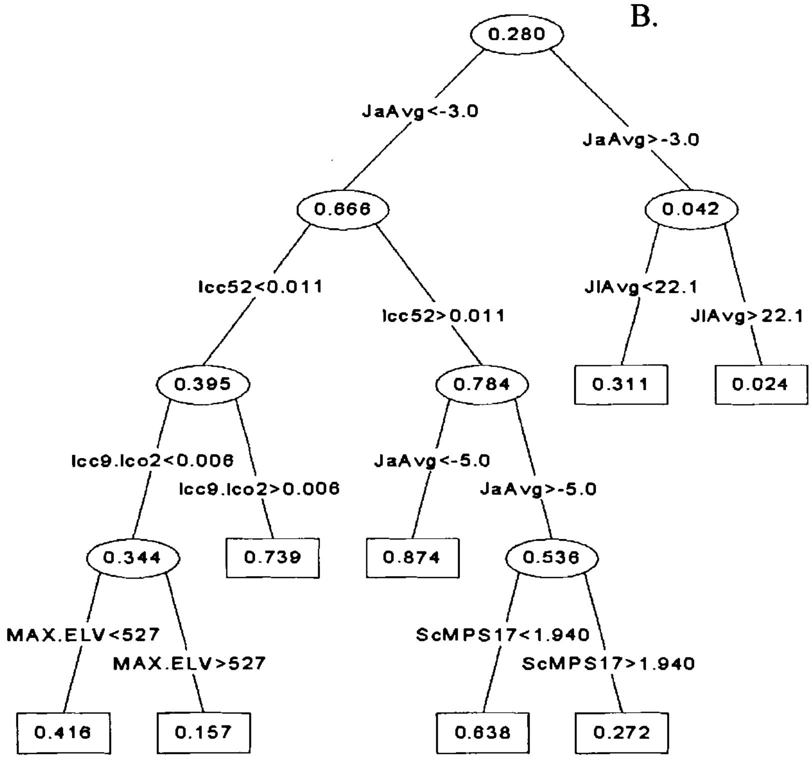

0.280
JaAvg<-3.0
JaAvg>-3.0
0.666
0.042
lcc52<0.011
lcc52>0.011
JlAvg<22.1
JlAvg>22.1
0.395
0.784
0.311
0.024
lcc9.lco2<0.006
lcc9.lco2>0.006
JaAvg<-5.0
JaAvg>-5.0
0.344
0.739
0.874
0.536
MAX.ELV<527
MAX.ELV>527
ScMPS17<1.940
ScMPS17>1.940
0.416
0.157
0.638
0.272

Table 1.2. Predictor variables that entered the rose-breasted grosbeak models (when modeled at the hexagon and county resolution) and the percent deviance in species occurrence explained by these variables. (an asterisks indicate the variable do not contribute to the model).

Variable name	100 R^2 of variables hexagon model	county model
Average patch size of land cover class 52, crop/woodland dominated by forage crops, hay, woodlots	48.0	*
Land cover class 136, northern mixed forest dominated by oak maple ash beech birch, jack pine and red pine	13.6	*
Average January temperature	10.3	71.1
Average seasonality index	3.3	*
Average elevation	2.6	*
Average July temperature	2.0	2.2
Land cover class 93, northern deciduous forest dominated by beech, birch, maple, oak, and pasture	1.7	*
Average patch size of land cover class 11, average patch size of Row crops dominated by corn and soybeans	1.0	*
Land cover class 52, Crop/woodland dominated by forage crops, hay, woodlots	*	8.9
Land cover class of Mixed(deciduous/coniferous)forests	*	1.5
Scaled maximum patch size in land cover class 17, row crops dominated by corn and soybeans	*	1.4
Maximum elevation	*	1.0
Total R^2	82.5	86.1

contributed over half of the total R^2 of the model. The only other variables that contributed greater than 10 percentage points were land cover class 136 (lcc136 -northern mixed forest dominated by oak maple ash beech birch, jack pine and red pine) and average January temperature.

The rose-breasted grosbeak model at the U.S. county resolution was different from the model at hexagon resolution. Here the root split occurred at an average January temperature (JaAvg) of –3.0°C (Figure 1.1b). It is clear that land cover class 52 in the root split of the hexagon model and the January climate threshold in the county model occupy overlapping areas in the study. However, any association of the land cover with January temperature would not be identified here as a simple cross-correlation because the difference in grain sizes between the models and the underlying patterns of variation associated with these variables will differ.

Only one out of six variables in the county model explained more than 10% of the variability in the species' occurrence in the eastern United States (Table 1.2). Unlike the hexagon model, average January temperature dominated the county model and contributed 71.1 percentage points to the total model R^2 of 86.1. Land cover variables (both coarse and fine resolution variables) contributed only 11.7 percentage points to the total R^2 (a relative contribution of 13.6% of the total R^2).

1.4.2 Summary of all species models

The total R^2 for hexagon and county resolution models of the seventeen species ranged from 50.3 to 80.2% and 59.6 to 87.7%, respectively (Table 1.3). I classified the variables that entered the models into four groups: climate, fine resolution land cover (160 land cover class metrics), coarse resolution land cover (14 land cover class metrics),

Table 1.3. Relative contributions for each species of climate variables, coarse (14-class) and fine (160-class) grained land cover variables (respectively), and other (landscape variables not attributed to the land cover classes) in the hexagon and county models.

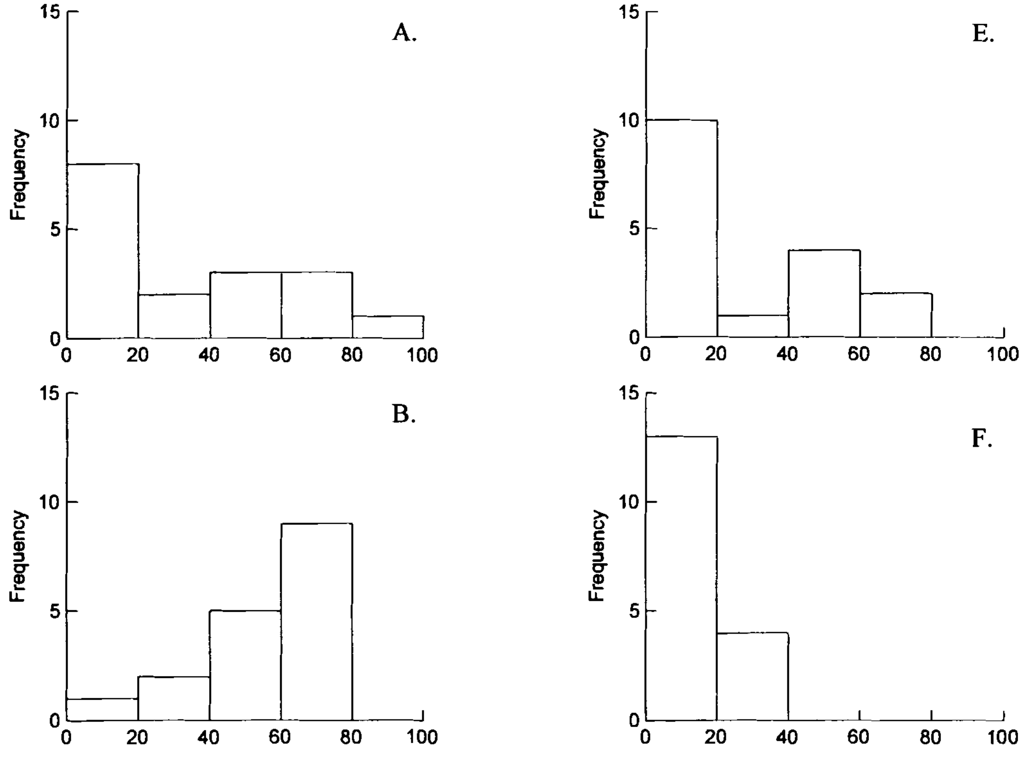
species	hexagon models					county models				
	total	climate	14-class	160-class	other	total	climate	14-class	160-class	other
Eastern wood-pewee	52.8	10.1	13.5	2.2	27.1	59.6	29.9	3.8	13.8	12.0
Least flycatcher	50.3	4.8	7.3	35.9	2.3	72.2	55.8	1.1	11.6	3.7
Orchard oriole	72.1	65.5	0.0	5.6	1.0	77.1	64.3	8.1	3.7	1.1
Baltimore oriole	77.1	54.2	2.2	1.6	19.2	84.9	76.2	0.0	8.7	0.0
Field sparrow	74.5	68.2	0.0	3.3	3.0	70.5	52.8	0.0	11.7	5.9
Northern cardinal	88.2	81.2	0.0	7.0	0.0	87.7	66.1	1.0	20.5	0.0
Rose-breasted grosbeak	82.5	15.6	0.0	64.2	2.6	86.0	73.3	1.5	10.3	1.0
Dickcissel	78.7	64.1	0.0	13.5	1.1	81.1	15.8	33.1	29.7	2.5
Summer tanager	76.4	20.8	5.5	48.2	1.9	87.0	78.3	5.6	3.1	0.0
Magnolia warbler	56.2	8.9	0.0	47.4	0.0	80.5	67.0	1.6	5.1	6.8
Black-thr. green warbler	63.4	22.6	0.0	40.8	0.0	79.1	69.0	1.3	7.5	1.3
Pine warbler	68.1	49.3	0.0	13.9	4.9	78.8	59.5	8.5	9.4	1.4
Prairie warbler	58.7	47.0	9.7	2.1	0.0	73.7	62.2	4.2	4.2	2.9
American redstart	62.9	2.4	0.0	60.5	0.0	74.5	55.6	13	3.4	2.5
Gray catbird	74.3	13.7	54.8	2.3	3.6	77.8	56.7	0.0	21.1	0.0
Brown thrasher	75.9	17.6	20.8	2.4	35.1	66.6	32.2	4.0	25.5	4.9
Blue-gray gnatcatcher	59.4	5.2	4.3	48.7	1.1	74.1	60.7	5.8	7.7	0.0
Mean	**69.1**	**32.4**	**14.8**	**23.5**	**8.7**	**77.1**	**57.4**	**6.6**	**11.6**	**3.8**

and other variables (landscape features other than vegetation land cover). The county resolution models were clearly dominated by climate variables with fourteen of the seventeen species models receiving approximately three-quarters of their total R^2 from climate variables (Figure 1.2, Table 1.3). Of the hexagon models for the seventeen species, seven models were dominated by climate variables, seven by the finely resolved land cover variables and three models contained a mix of all variable classes (Table 1.3). Thus, the increase in the grain size from hexagons to counties resulted in a shift from a more balanced contribution by land cover, landscape and climate variables to a heightened importance of climate variables (Figure 1.2).

The total R^2 increased in 14 of the 17 species' models with the switch from hexagon to county grain models. There was an average within species increase of 8.0 (± 8.9 SD) percentage points of the total R^2 from hexagon to county models. The increase was greatest in hexagon-based models that explained less than 70 percent of the total species variation, with gains of 7-24 percentage points (Figure 1.3). Five of the eight species in this category had hexagon models that were dominated by land cover variables (Table 1.3.).

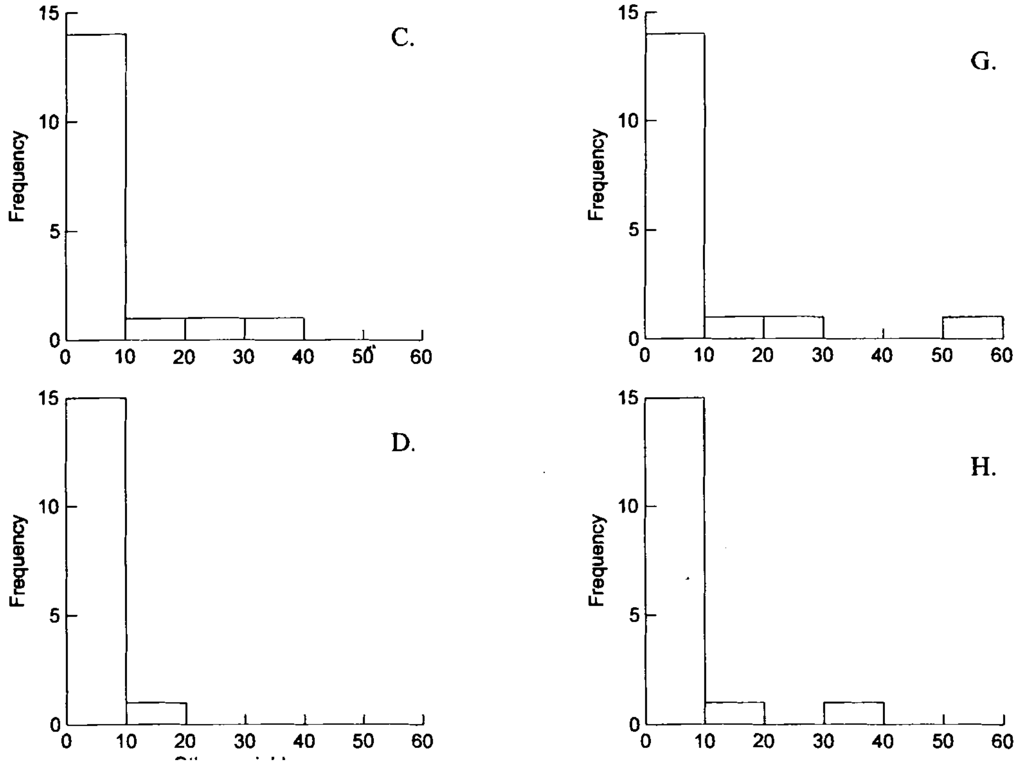
The larger increases in the R^2 values of the county resolution models for species with R^2 values < 70% in the hexagon models (leftmost species in Figure 1.3) might be connected to differences in their autocorrelation patterns relative to those species with R^2 values > 70% on the (rightmost species). The semivariograms indicate a clear pattern in the spatial organization of the two groupings (R^2 values > 70% and <70% in hexagon models; Figure 1.4). Species with hexagon models total R^2 below 70% had flatter sample semivariograms and a more narrow range in semi-variance across the United States than

Figure 1.2. Frequency distribution of the percent deviance explained from climate variables (A, B), fine resolution land cover classes (160 class) (E, F), coarse-grained land cover classes (14 class) (C, D), and other variables (landscape variables not attributed to the land cover classes) (G, H) in the species models at hexagon (A,C,E,G) and county resolution (B,D,F,H) respectively.



Climate variables

lcc 160 variables



Other variables

lco2 variables

Figure 1.3. The total percent deviance explained in the individual species abundance from the county-based models in relation to the corresponding hexagon-based model. The line corresponds to equal deviance explained.

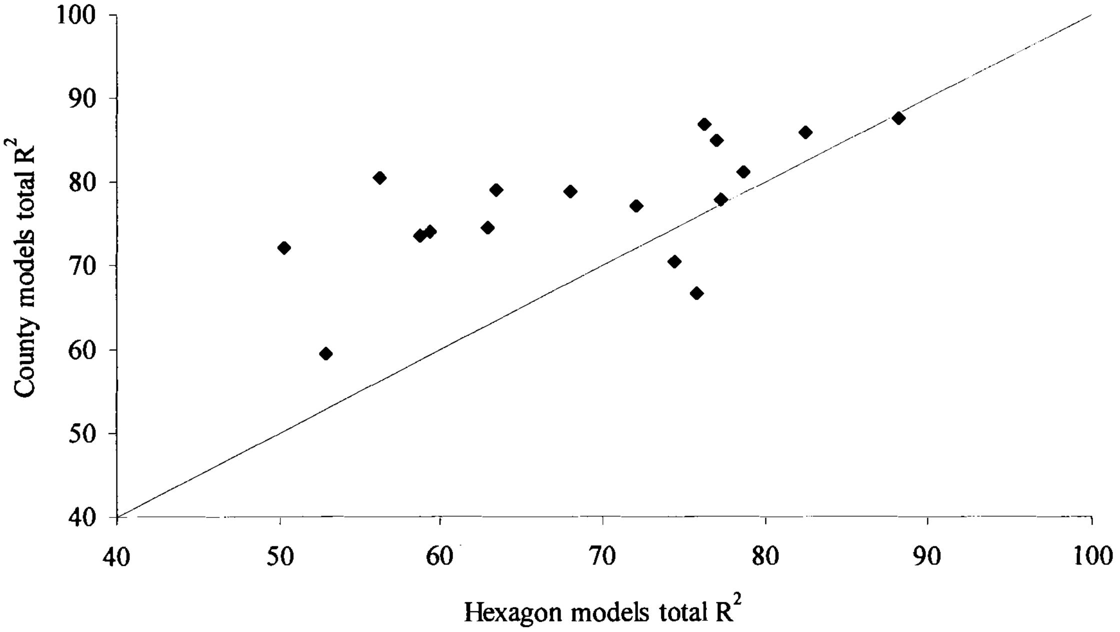
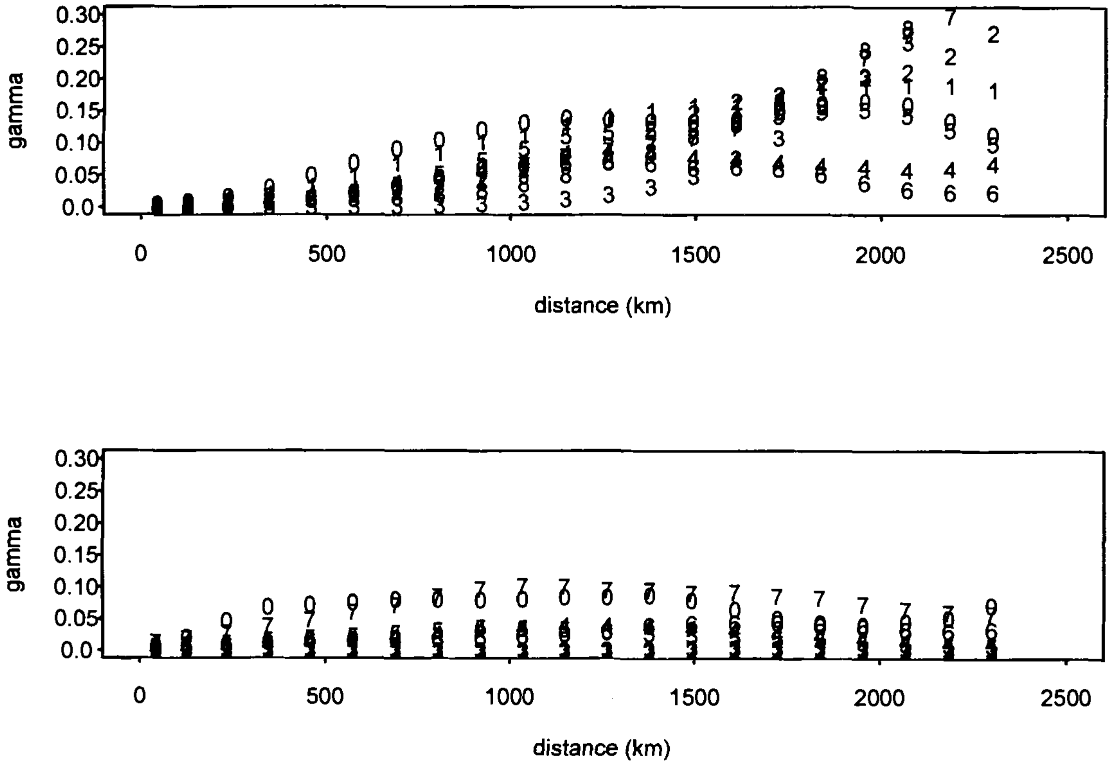


Figure 1.4. Semivariograms for each species abundance at the hexagon resolution. The estimated semi-variance (gamma) is plotted against the distance (km) between data points. The upper plot contains the species with hexagon models that had total R^2 greater then 70 % (0 represents the orchard oriole, 1 baltimore oriole, 2 field sparrow, 3 northern cardinal, 4 rose-breasted grosbeak, 5 dickcissel, 6 summer tanager, 7 gray catbird, 8 brown thrasher). The bottom plot contains the species models that had a total R^2 below 70% (0 represents the eastern wood-pewee, 1 least flycatcher, 2 magnolia warbler, 3 black-throated green warbler, 4 pine warbler, 5 prairie warbler, 6 american redstart, 7 blue-gray gnatcatcher).



the models with $R^2 > 70\%$. To further investigate the autocorrelation possibility, the semivariograms were used to produce estimates of the range (distance) over which the data were spatially correlated for each of the species. The range estimate identifies the distance at which data points become independent (Maurer 1994). In order to estimate this range of spatial correlation I identified 90% of the maximum semi-variance on each species' sample semivariogram and then recorded the distance at which this intersection occurred (Table 1.4). Due to insufficient data, there were three species (least flycatcher, magnolia warbler, black-throated green warbler) for which the range of spatial correlation could not be estimated. These species have relatively small distributions in the conterminous United States, and are restricted to the northeast and along the Appalachian Mountains south to North Carolina. In the remaining fourteen species there was a positive relationship between the hexagon model total R^2 and these estimated spatial auto-correlation ranges ($r_s = 0.561$, $r_{s0.05(2)14} = 0.538$, $P < 0.05$). This association suggests that as the range of spatial correlation increase (indicating a more homogonous or broader distribution) there is an increase in model predictability.

The differences in variable contribution and total model explanatory ability between the 17 bird species models at the hexagon and county resolutions appear to be a result of the change in grain size. As noted above, a potential bias in such a conclusion was that spatially interpolated data from Yang et al. (1995) were used in cross-walking the data to the county resolution. The model constructed with the comprehensive data were positively correlated with the 17 species hexagon models ($r_s = 0.738$, $r_{s0.05(2)17} = 0.485$, $P < 0.05$). More importantly, these models show the same landscape dominated model characteristics as the original hexagon based models, and only five of the 17

Table 1.4. The total R^2 from the 640 km^2 hexagon models, and the estimated distance at which the species abundance data were no longer correlated upon themselves. Range estimates were identified at the intersection of 90% of the maximum semi-variance (gamma) and the trend of the semivariogram line. (an asterisk indicates that no range estimate could be made from the sample semivariogram).

Species	Total R^2	Range estimate (km)
Least flycatcher	50	*
Eastern wood-pewee	53	600
Magnolia warbler	56	*
Prairie warbler	59	800
Blue-gray gnatcatcher	59	800
Black-throated green warbler	63	*
American redstart	63	1400
Pine warbler	68	900
Orchard oriole	72	1800
Gray catbird	74	1600
Field sparrow	74	2200
Summer tanager	76	2100
Brown thrasher	76	1000
Baltimore oriole	77	2100
Dickcissel	79	1700
Rose-breasted grosbeak	83	1100
Northern cardinal	88	2000

species models were dominated by climate variables. Hence the dominance of climate variables in county models (14 of 17) cannot be attributed to a bias from complete bird coverage.

1.5 Discussion

Several previous studies have discussed the influence of spatial grain on the description of species distributional patterns and how observed patterns change at different grain (e.g., Clark 1985, Wiens 1989, Maxwell and Costanza 1994). The changes in patterns with varying grain suggested by these studies was confirmed here in the differences in predictor variables selected by the fine-grained hexagon and the coarse-grain county models for bird species' distributions (Figure 1.2). The county resolution models had an average R^2 of 77.1 % and were dominated by climate variables, which accounted for on average 57.4 percentage points of the total R^2. In contrast, the hexagon models had fairly equal contributions of climate and land cover variables (averaging 32.4 and 36.7 percentage points, respectively).

The high influence of long-wave climate variables in the county models can be attributed to a general decrease in between-point variability with an increase in spatial grain (Wiens 1989, Jelinski and Wu 1996). This decrease in variability of the data set hides underlying variation that would be detected at finer resolution and thus provides an opportunity for long wave climate variables to dominate the models by efficiently explaining most of the coarse-grained variability (the only variability present to be explained). The coarse-grained relationships between climate and bird distributions reflect physiological determinants of many bird species ranges (Root 1988b), indicating that projected climate change could have the potential to greatly influence bird species distributions.

Climate variables are, however, not the only environmental determinants that constrain bird species distribution. Habitat condition is also an important component shaping species distributions. In this analysis, land cover and elevation variables were clearly important in the hexagon model, but even at the county grain, where climate variation comprised most of the species model explanatory ability, land cover and elevation variables did describe some portions of the species distribution in each of the models. This highlights the importance of including climate and land cover, and elevation variables when modeling species occurrences even at coarse-grains. This result provides further evidence that it will be necessary to include both climate and vegetation distributions into projections of bird distributions under future conditions if we hope to gain an accurate picture of the birds' potential responses to global climate change (Root and Schneider 2002).

The loss of variability in bird occurrence data with a coarser spatial grain increased the overall model predictability, as described by Maxwell and Costanza (1994). The total R^2 increased for fourteen out of the seventeen species models when the spatial grain was increased from hexagons to counties. However, the difference in total model R^2 at the two spatial resolutions was not uniform across all species, thus resulting in a wide range of differences between hexagon and county resolution models. The bird species models at the hexagon resolution that explained less then 70% of the species' occurrence showed a greater increase in total R^2 as the grain was increased (Figure 1.3). A possible explanation for the uneven increase in model predictability with the change in resolution may be the spatial autocorrelation in the data. The estimates of the semi-variance range - the maximum distance at which species incidence data points were correlated spatially - increased with the total R^2 of the species' hexagon models. If local abundances of species within their ranges are spatially autocorrelated, then such correlations will affect the relative magnitude of variance measured at hexagon and county resolution (Maxwell and Costanza 1994) and therefore the relative explanatory power of the two models. All nine species with total R^2 above 70% in their hexagon models had relatively large estimates of autocorrelation ranges (above 1000 km), making them less sensitive to the integrating effect of the coarser-grain. The lower maximum distance of correlation between data points from species with total R^2 values below 70% in their hexagon models, on the other hand, indicates that these species are more localized (Koenig 2001) and therefore more sensitive to the effects of increases in grain. The only exceptions to this pattern was the American Redstart, which had a larger range but a lower hexagon model total R^2.

Although this study provides insight into the influence of spatial resolution in modeling bird species occurrences, it is not an exhaustive analysis of the influence of climate variables on modeling all bird species in the eastern United States. However, the species included in this analysis were selected by taking into account a wide variety of important considerations in modeling bird distributions (e.g., the range size of the species, climate dominated models, and land cover and elevation dominated models). It is, therefore, rather unlikely that this analysis resulted in a systematic bias and the results found here can be applicable to other species.

My results indicate that bird species distribution models can be confidently constructed in the eastern United States at the county resolution. Iverson and Prasad (1998) created projections of potential future distributions of 80 individual tree species in the eastern United States under five GCM scenarios at the United States county resolution. By integrating their projections for future tree species distributions with climate predictions of GCMs the potential response of bird species to a rapidly changing climate and vegetation patterns can be modeled. However, a necessary intermediate step, developed in Chapter 2, is to verify that the replacement of the predictor variables selected in my analysis with the individual tree species data and climate variables used by Iverson and Prasad (1998) still results in acceptable models of bird species occurrences.

Chapter 2

EFFECTIVENESS OF TWO CLIMATE DATA SETS AS PREDICTORS OF BIRD DISTRIBUTIONS

2.1 Abstract

Attempts to predict avian species responses to global climate change rely on General Circulation Model (GCM) outputs. These climate models are commonly created to depict future climate conditions, but they are based on physical processes at very coarse-grain. Before future projections of species distributions can be made, it is desirable to examine the appropriateness of modeling current species distributions with variables that can be obtained from GCM outputs. The present study assessed the ability of climate variables obtained from thirty year means (which constitute empirical data equivalents of the climate variables obtained from GCM models) to model the contemporary distributions of some 17 bird species. I compared the species models using these GCM input climate variables to species models using climate variables that have previously been successfully used in ecological studies to explain species distributions (Root 1988a and O'Connor et al. 1996). I thus assessed the effectiveness of the 'GCM input variables' in modeling avian species occurrences.

A principal component analysis including both sets of climate variables revealed two independent sources of variation in the data. The first component explained 70% of the variation in the climate data and represented seasonality patterns along a strong north to south gradient across the study area (the conterminous U.S. east of the 100th meridian). The second component explained 19% of the variation and represented the influence of July temperature and potential evapotranspiration along an east-west gradient across the eastern United States.

Using regression tree analysis, I constructed three sets of models for each of the 17 bird species using the GCM input and conventional climate data. I constructed one group of models with just the GCM input climate variables (GCM input set), one with just the climate variables from previous ecological studies (conventional set), and one with both sets of climate variables available as potential predictors (composite set). In each of these three sets of models the same land cover and landscape variables were included as potential predictors.

There was little difference in total R^2 between the models for each species. The largest (but non-significant) difference in total R^2 was between the models containing conventional and GCM input variables (mean ± SD = 1.7 ± 3.2 percentage points). Climate variables were dominant in all three sets of models, but their elative importance differed between GCM and conventional models (Wilcoxon signed rank test, $P = 0.025$). In the composite models, conventional climate variables appeared in all 17 species models, with an average contribution of 42 percentage points to the average total model R^2 (76.8%), while the GCM data set occurred in only 9 of the composite models and contributed a mean of 29 percentage points to the total model R^2. GCM input variables thus performed well in modeling species distributions when other land cover variables were also present, but by themselves were not adequate surrogates for the conventional climate variables.

2.2 Introduction

Although changes in the Earth's climatic patterns are constantly occurring, mounting evidence suggests that current global warming will continue to be faster than episodes of climate change over the last 1000 years (Root and Schneider 2002). Given increased evidence of rapid global climate change, research has begun to focus on understanding the potential consequences of this changing environment for wildlife (Kareiva et al. 1993, Price and Root 2000,and Walther et al. 2002, Root and Schneider 2002).

Most predictions of species responses to climate change rely on general circulation models (GCM) (Iverson and Prasad 1998, Price and Root 2000, Sorenson et al. 1998). GCMs are typically created at very broad scales and are used to gain information about global climate patterns and processes (Schneider et al. 1992, Gates 1993). Through continued refinements, a rapid and efficient evolution of GCMs has led to consistent predictions of current and past climatic conditions (McAvaney et al. 2001). These models also are used to predict future climate changes. Most recent GCMs project an increasing global temperature under scenarios of doubling atmospheric CO_2 concentrations (Baede et al. 2001).

GCMs are based on current understanding of the complex interactions of physical processes occurring on the planet (Gates 1993). The variables used as inputs into these simulations reflect important components that drive climate patterns, such as atmospheric conditions, moisture patterns, and prevailing winds that mix the entire system (Gates 1993). These models are commonly designed to output climate variables that can represent long-term climate patterns and are typically assessed by comparison against empirical averages compiled over thirty years of climate data.

Early biogeographic models related species diversity to coarse-grain climate patterns (Ashmole 1963, Simpson 1964, and Kiester 1971). For birds these ideas have been pursued further and the role of climate in determining regional and continental patterns of species distributions and richness has been identified (O'Connor 1996, Root

1988a, Currie 1991). Bird studies have typically used coarse-grained climate variables to explore the extent to which winter survival might be determined by average temperature (Root 1988b) and to explore how breeding distributions relate to resource availability, as characterized by seasonal climate patterns (Ashmole 1963). The choice of climate variables in these studies was driven by specific biological questions and revealed important coarse-grained influences on species assemblages. These conventional climate variables are however, rather different from the types of climate variables readily available from GCM outputs. It is, therefore, desirable to evaluate the effectiveness of these GCM climate variables in modeling bird distributions before using them to make projections of the species distributions likely under onto climate change scenarios.

The goals of this analysis were therefore to identify whether the type of climate variables commonly available from GCM outputs and the type of climate variables typically used in conventional bird studies were equally effective as predictors in bird abundance models, and to quantify any differential effects present in the use of the two climate data sets. For this analysis I compared thirty-year averages of the conventional climate variables to the climate variables commonly found in GCM outputs. The term 'conventional climate variables' will be used to reference long term, average, climate variables that have been used in previous ecological studies of environmental determinants of bird species patterns. The term 'GCM input climate variables' will be used to identify current long-term, average, climate conditions organized into the metrics that are commonly used as the baseline for GCM and thus represent the variables available from GCM outputs. These two climate data sets should overlap in their predictions to some degree because they both characterize climate patterns at coarse-grains. If the variables of GCM input climate data prove to be equal or even better at describing current bird species distributions, then projections onto GCM scenarios of future climate conditions can be made with confidence. If they prove to be inferior in predicting bird distributions, on the other hand, a significant limitation to the use of GCM scenarios in projecting future wildlife distributions will have been identified. And the types of variables that are output from GCM scenarios may need to be reorganized to produce variables that are more appropriate to predicted species patterns.

2.3 Methods

The spatial extent of this study was the eastern United States (east of the 100th meridian), and the grain size was U.S. counties. This extent and grain provided a scale broad enough to highlight climate patterns, yet fine enough to model individual bird species within their range. The problem of variation in the size of counties across the United States was minimal here, given the relatively fixed county size in the eastern U.S. (Iverson and Prasad 1998).

The analyses comprised four steps, which are described in more detail in subsequent sections. 1) Seventeen bird species representing a cross-section of well-understood continental bird distributions previously modeled on a fine resolution spatial grid (in 640 km^2 hexagonal cells of the EMAP grid of White et al. (1992)) were selected to provide a broad array of conditions over which the performance of GCM input and the conventional climate variables could be compared. 2) The bird species abundance and predictor variables of the hexagonal data frame were cross-walked to county units. The effects of this change in spatial scale have been investigated in a separate set of analyses (see Chapter 1). 3) Principal component analysis was used to assess the relatedness of the two independent sets of climate variables (i.e., conventional and GCM climate variables). 4) Regression tree analysis was used to construct models of the seventeen species abundance with the two climate data sets.

2.3.1 Data

The data for the individual species came from the national Breeding Bird Survey (BBS) (1981-1990). O'Connor et al. (1996) aggregated the incidence of each of 615 species to the EMAP grid at the spatial resolution of 640 km^2 hexagons across the conterminous United States. For each of these hexagons an incidence value - the proportion of surveys on the corresponding BBS route in which the species was recorded - was compiled. These incidence values are interpreted as an absolute abundance here, given the typical relationship between incidence and abundance for most organisms (e.g. Hanski 1992 and Maurer 1990). They could not be converted to express measures of density because the (species-specific) slope linking incidence and abundance for each species was unknown.

Seventeen species (Table 2.1) were chosen to reflect important considerations in modeling species occurrence with the two sets of climate variables. First, the species model had to account for at least 50% of the variation in incidence, to ensure that the evaluation of the GCM variables was against a practical model: the preliminary models ranged in total R^2 from 50-88%, thus providing a range of model goodness-of-fit. Second, the group of bird species represented a cross-section in the types of predictor variables selected in their models. Some species models were dominated by climate variables, some by land cover variables, and other species had a balance of climate and land cover variables. Finally, the seventeen species selected were individually associated with a range of habitats, ranging from old fields to forest interiors.

Table 2.1. List of the species included in this study.

Species
Eastern wood-pewee (*Contopus virens*)
Least flycatcher (*Empidonax minimus*)
Orchard oriole (*Icterus spurius*)
Baltimore oriole (*Icterus galbula*)
Field sparrow (*Spizella pusilla*)
Northern cardinal (*Cardinalis cardinalis*)
Rose-breasted grosbeak (*Pheucticus ludovicianus*)
Dickcissel (*Spiza americana*)
Summer tanager (*Piranga rubra*)
Magnolia warbler (*Dendroica magnolia*)
Black-throated green warbler (*Dendroica virens*)
Pine warbler (*Dendroica pinus*)
Prairie warbler (*Dendroica discolor*)
American redstart (*Setophaga ruticilla*)
Gray catbird (*Dumetella carolinensis*)
Brown thrasher (*Toxostoma rufum*)
Blue-gray gnatcatcher (*Polioptila caerulea*)

The first set of potential predictors for bird species' models, which I call the conventional climate variables, was adopted from O'Connor et al. (1996). The climate variables in this data set reflected metrics that have been used in previous studies to explore the influence of climate on bird species (O'Connor et al. 1996, Root 1988a). They included long-term climate variables such as July temperature, January temperature, annual precipitation, and average seasonality (difference between July and January temperature).

The other set of climate variables included in the analysis were the GCM input climate variables used by Iverson and Prasad (1998) to model current tree species distributions at the county grain. They were derived from forty-year monthly means and represent the variables that could be obtained from future forecasts of climate conditions through GCMs. Variables in this data set included average precipitation, average monthly temperatures for July and January, potential evapotranspiration (PET), the difference between July and January temperature, the July-August ratio of precipitation to potential evapotranspiration, the average temperature from May to September, and the average yearly temperature.

In addition to the climate variables, landscape features were incorporated as potential predictors of species abundance. This data set included land cover classes (Loveland et al. 1991) represented at two degrees of descriptive resolution (160 classes and 14 classes), spatial organization of these land cover classes (i.e. patch sizes), and additional landscape metrics (e.g., length of road, length of riparian systems, and elevation). Since many bird species show strong habitat relations within broader areas of suitable climate, these landscape variables provided the necessary habitat information.

2.3.2 Cross-walking from hexagon to county resolution

The bird species data, landscape variables, and the conventional climate variables were cross-walked to the county grain to match the resolution as the GCM input variables. Variables were converted to the county grain by overlaying the EMAP hexagonal grid with a U.S. county boundary layer. Polygons were identified at the intersection of the hexagons and counties. Then a data frame was produced with the vectors identifying the area of each polygon, the hexagon and county identities associated with that polygon, and the value of the variable at the hexagon-grain that was being cross-walked. For proportional data (such as the bird species incidence and the land cover class), polygons were assigned the proportional value from the hexagon it was associated with, and the polygons were then area-weighted by its relative contribution to the county. These weighted values were then summed within each county to arrive at the county-level estimate (Matthews et al. 2002). In order to cross-walk the average patch size of each land cover variable, it was necessary to account for the number of 1 km^2 pixels in a polygon in addition to the area of the polygon. By finding both of these areas, the estimate of the county level average patch size was more accurate because it was weighted by the polygon area and the relative amount of land cover present in the county.

Finally, four climate variables in the hexagon data set - January temperature, July temperature, seasonality and precipitation - along with the elevation variables were each represented by three measures (averages, minima and maxima). These variables also needed to be cross-walked. For maximum and minimal values, I identified the polygon within each county that had maximum and minimum values for each variable value and assigned these values to the county. The average metrics were cross-walked by area-weighting the polygons in each county, multiplying this area weight by the average values associated with that polygon, and summing within the county to arrive at the county-level estimates.

2.3.3 Analyses

To compare the congruence of conventional and GCM input climate variables as to their ability to describe mutually independent areas of variation, I conducted a principal component analysis (PCA) on the correlation matrix containing variables from both data sets. The PCA provided information about the relationships among the two sets of climate variables.

To evaluate the effectiveness of the two sets of climate data in modeling individual bird species abundance I used regression tree analysis (Breiman et al. 1984) in S-Plus, Version 6 (Insightful 2001). Unlike traditional regression methodology, the regression tree procedures do not rely on linear combinations of variables for associating dependent and independent variables. Therefore, they are able to handle non-linear interactions among variables without a priori specification of such interactions and are not constrained by strict assumptions about the underlying data distributions (Iverson and Prasad 1998, Clark and Pregibon 1992).

Regression tree analysis produces a model by recursively partitioning the dependent variable by a "best fitting" independent variable (Clark and Pregibon 1992). The algorithm orders the sample by the values of each predictor variable in turn and searches through all possible binary splits along that ordering; it accepts the split at the point for which the predictor maximizes the difference in the response variable between the two subsets. This process continues independently and recursively on each of the two sub-samples formed at each node until pre-selected stopping criteria are reached. At this point, the model is over-fit (De'ath and Fabricius 2000, Verbyla 1987) and cross-validation procedures are used to prune the resulting tree model back to an optimal number of end nodes. To avoid using over-fit models, I used the minimum deviance tree in conjunction with a 1.0% node deviance minimum, which in these data sets closely approximates the "one standard error" cross-validation procedures of Breiman et al. (1984). This procedure has been found in simulations to produce optimally sized models with our data (J. Sifneos personal communication). To identify any locally correlated variables that introduced collinearities into any subset of the tree, each of the variables in the resulting model was perturbed in turn (data points of the perturbed variable were randomly changed with each point having an equal chance of being selected) by an average of 5 % and the model was re-run. For each of the predictor variables that occurred in the model, and additionally for the overall regression tree, the model goodness-of-fit was reported as the percentage of the mean square deviance explained; this measure was represented by $100*R^2$ values.

Three models were created for each species. The first included both the GCM input climate variables and the landscape (land cover and elevation) variables as potential predictors. The second model was created for each species using the conventional climate variables, together with the same landscape (land cover and elevation) variables, as potential predictors. These two models in effect allowed estimation of the extent to which either could substitute the other. However, I could not unequivocally evaluate the incremental information gained or lost on using the GCM input climate variables instead of the conventional climate variables. It was, therefore, necessary to run a third regression tree model for each species: this included both sets of climate data along with the landscape data as potential predictors of the species abundance. This set of models put the two climate data sets into competition with each other in order to provide a better understanding of the relative performance of the GCM input variables. These models are hereafter referred to as composite species models.

2.4 Results

The conventional and GCM input climate data sets combined contained 20 climate variables, and many of these variables were strongly associated with each other (Table 2.2). In the GCM input data set, potential evapotranspiration (PET) and the mean May to September temperature (MAYSEPT) correlated highest with measures of July temperature (JULT and JlAvg). Average yearly temperature (AVGT) was positively correlated with mean January temperature (JANT and JaAvg), while all measures of seasonality were negatively associated with January temperature. Furthermore, the measures of minima and maxima for July, January, precipitation, and seasonality were all highly associated with their corresponding mean metrics.

Mean precipitation (PPT and PptAvg), mean July temperature (JULT and JlAvg), mean January temperature (JANT and JaAvg) and mean seasonality (SeasAvg and JUL.JANT) were entered only once into the PCA because they were essentially the same pairs of variables present in both data sets. In general, correlations between these like measures in the conventional and GCM input climate data sets were high but not identical because of minor heterogeneities generated in the cross-walking process and because the data came from slightly different time periods. The weakest relationship between two supposedly identical variables was between average July temperatures, which captured 84.6% of the variation in the data (r = 0.92). Success in cross-walking would be expected to vary geographically if the variables involved have some spatial heterogeneity and this was in fact observed. Differences in the conventional and GCM input measures of July

Table 2.2. Correlation matrix of the climate variables used in this analysis. The horizontal and vertical lines separate variables stemming from the conventional data set from the GCM input climate variables (n=2121).

	JANT	PET	JULT	PPT	AVGT	MAYSEPT	JULJANT	JARPPET	JaAvg	JaMn	JaMx
JANT	1.000										
PET	0.567	1.000									
JULT	0.735	0.848	1.000								
PPT	0.813	0.209	0.468	1.000							
AVGT	0.966	0.705	0.882	0.737	1.000						
MAYSEPT	0.842	0.810	0.982	0.586	0.952	1.000					
JULJANT	-0.923	-0.279	-0.419	-0.824	-0.795	-0.572	1.000				
JARPPET	0.137	-0.526	-0.395	0.335	-0.038	-0.259	-0.407	1.000			
JaAvg	0.998	0.563	0.736	0.816	0.965	0.842	-0.921	0.148	1.000		
JaMn	0.966	0.577	0.770	0.731	0.960	0.865	-0.858	0.091	0.968	1.000	
JaMx	0.991	0.539	0.700	0.839	0.945	0.811	-0.931	0.182	0.993	0.942	1.000
JlAvg	0.821	0.819	0.925	0.527	0.917	0.946	-0.576	-0.259	0.823	0.868	0.782
JlMn	0.615	0.660	0.791	0.279	0.732	0.794	-0.376	-0.272	0.617	0.769	0.547
JlMx	0.843	0.817	0.886	0.616	0.914	0.918	-0.627	-0.194	0.846	0.836	0.835
PptAvg	0.826	0.228	0.483	0.997	0.752	0.601	-0.833	0.336	0.829	0.745	0.852
PptMn	0.855	0.277	0.562	0.969	0.805	0.673	-0.827	0.266	0.858	0.811	0.862
PptMx	0.713	0.136	0.328	0.937	0.612	0.445	-0.769	0.383	0.716	0.573	0.760
SeasAvg	-0.952	-0.348	-0.532	-0.855	-0.855	-0.669	0.974	-0.343	-0.954	-0.886	-0.965
SeasMn	-0.938	-0.338	-0.516	-0.854	-0.839	-0.652	0.964	-0.342	-0.939	-0.866	-0.957
SeasMx	-0.953	-0.350	-0.539	-0.850	-0.859	-0.676	0.972	-0.338	-0.954	-0.893	-0.964

	JlAvg	JlMn	JlMx	PptAvg	PptMn	PptMx	SeasAvg	SeasMn	SeasMx
JaAvg									
JaMn									
JaMx									
JlAvg	1.000								
JlMn	0.873	1.000							
JlMx	0.942	0.724	1.000						
PptAvg	0.547	0.295	0.636	1.000					
PptMn	0.635	0.438	0.673	0.973	1.000				
PptMx	0.371	0.041	0.516	0.940	0.861	1.000			
SeasAvg	-0.614	-0.395	-0.677	-0.863	-0.856	-0.799	1.000		
SeasMn	-0.597	-0.358	-0.664	-0.862	-0.850	-0.806	0.989	1.000	
SeasMx	-0.623	-0.412	-0.677	-0.858	-0.856	-0.788	0.996	0.983	1.000

temperature occurred exclusively along large bodies of water (Atlantic Ocean, Gulf of Mexico, and Great Lakes) and in some areas along the Appalachian Mountains. These areas could be expected to have large variability in climate over small areas because of the climatic influences of large water bodies and sharp elevational gradients. Even so, of the 2121 counties in this study, only 130 (6.1%) showed differences between the conventional and GCM input metric of average July temperature greater than 1 degree Celsius.

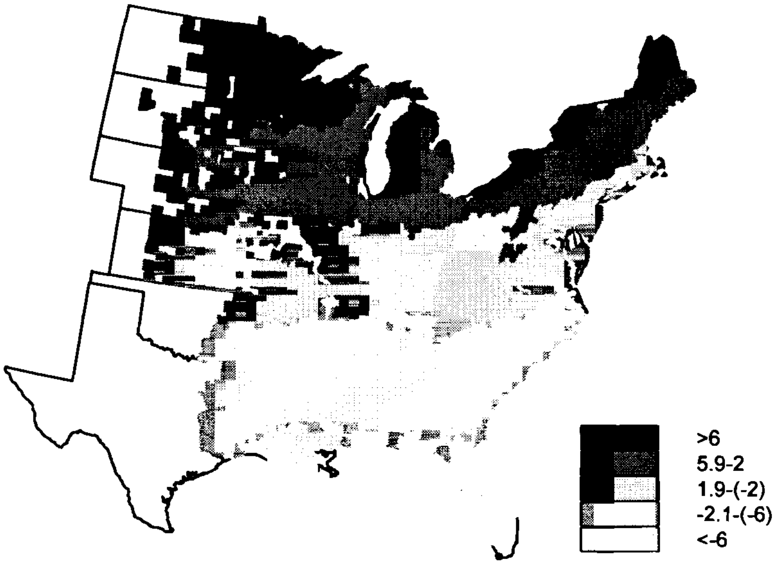
The PCA reduced the climate data sets to two significant components that captured 90% of the variation in the data (Table 2.3). Loadings on like variables (e.g., the metrics of seasonality JUL.JANT, SeasMn and SeasMx) were similar (Table 2.3), indicating that the two data sets have similar functional relationships. The first component accounted for 70.6% of the variation in the climate data. The only positive loadings on this component were from the measures of seasonality. Measures of January temperatures and average yearly temperature were the most influential factors of the negatively loading variables. This first component highlighted the broad-scaled climatic influences along the north to south gradient (Figure 2.1) and represented patterns of seasonal climate and winter temperatures in the eastern United States. The second component had an eigenvalue of 3.060 and explained 19.1% of the variation in the climate data (Table 2.3). July temperature and potential evapotranspiration had the highest positive loadings, while the ratio of July to August precipitation with potential evapotranspiration (JARPPET) had a strong negative association (Table 2.3). The second component captured the east to west gradient and identified major landforms (i.e. local climates) in the eastern United States with similar climatic patterns across a wide variety

Table 2.3. Climate variable loadings in the principal component analysis. Component 1 accounted for 70.6 % and component 2 accounted for 19.1% of the variation in the climate variables. The eigenvalues for component 1 and 2 were 11.291 and 3.060, respectively.

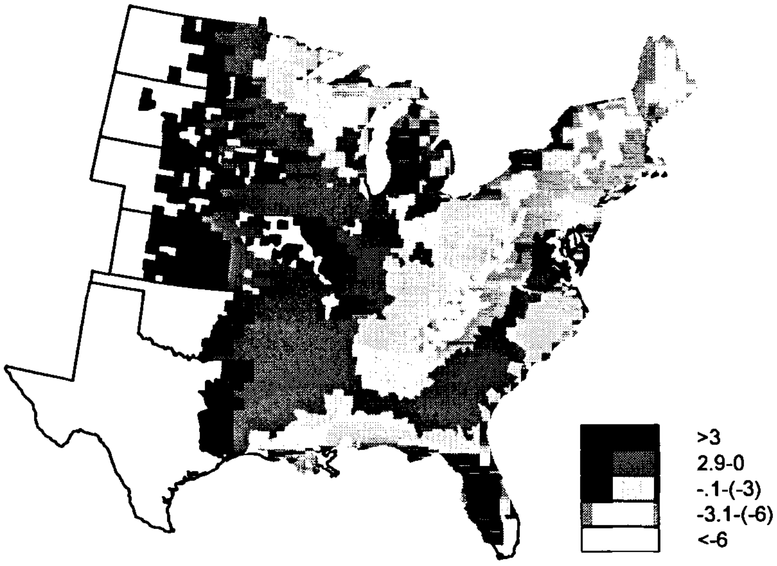
	component 1	component 2
Mean January temperature (JANT)	-0.294	-0.028
Potential evapotranspiration (PET)	-0.180	0.397
Mean July temp. (JULT)	-0.235	0.322
Annual precipitation (PPT)	-0.250	-0.234
Mean annual temperature (AVGT)	-0.292	0.100
Mean May-September temp. (MAYSEPT)	-0.263	0.244
Difference in July and January temp. (JUL.JANT)	0.261	0.220
July-August ratio of precipitation to PET (JARPPET)	-0.027	-0.482
Minimum January temperature (JaMn)	-0.286	0.038
Maximum January temperature (JaMx)	-0.293	-0.063
Minimum July temperature (JlMn)	-0.192	0.321
Maximum July temperature (JlMx)	-0.263	0.200
Minimum precipitation (PptMn)	-0.263	-0.167
Maximum precipitation (PptMx)	-0.218	-0.297
Minimum seasonality (SeasMn)	0.271	0.192
Maximum seasonality (SeasMx)	0.275	0.177

Figure 2.1. Maps of the scores for the two significant components from the principal component analysis, showing the north to south gradient of the scores in component 1, and a more east to west gradient in component 2.

component1



component2

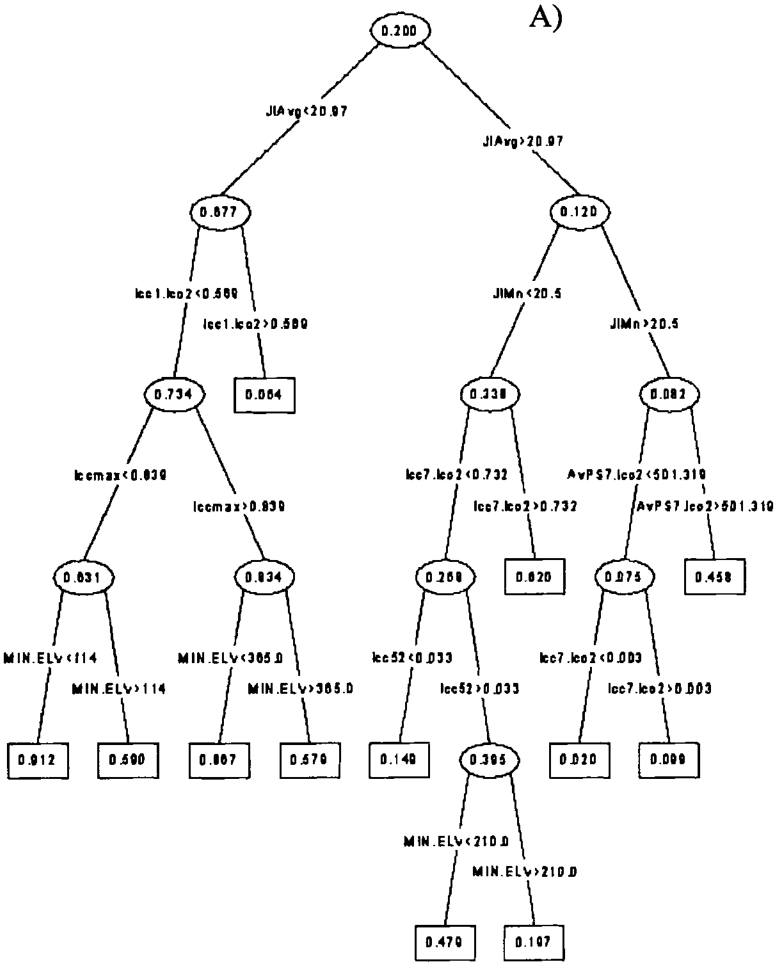


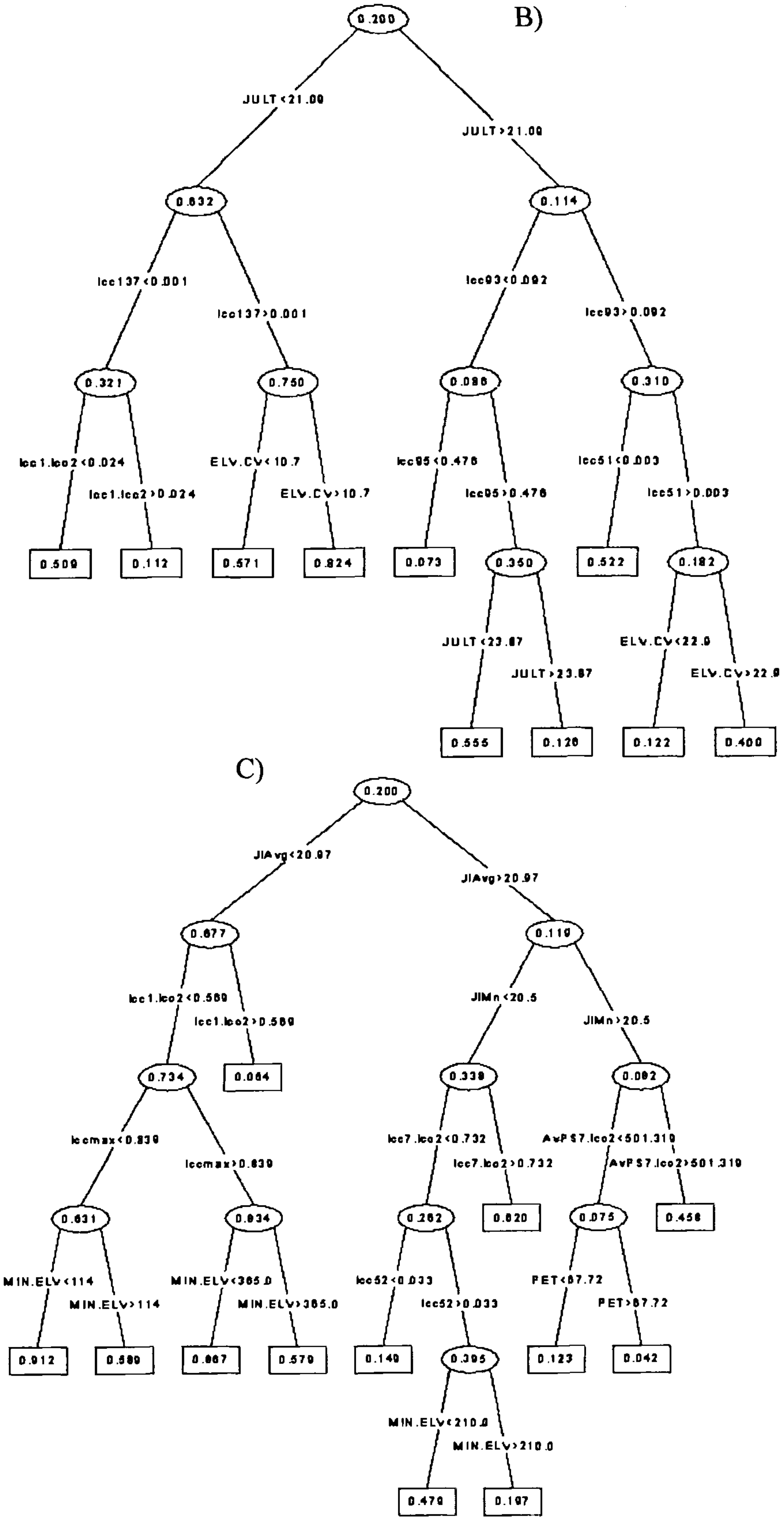
of variables. The congruence between equivalent variables from the two data sets therefore indicated that the broad climate patterns were adequately captured by both data sets and that the differences were largely due to local aggregation errors in the cross-walking from the fine-grained data.

2.4.1 Species models

Before summarizing the regression tree models for all seventeen bird species, I present detailed results for a single species, the American redstart (Setophaga ruticilla), in order to explain the regression tree results in detail and to bring the analysis into clearer focus. In the American redstart model created with the conventional climate data, the first split in the species data occurred at a threshold in average July temperature of 20.97 °C (Figure 2.2a). The right hand branch of this root split contained locations with warmer July temperatures, and predicted a mean occurrence of 0.120 for the American redstarts (i.e. the species was recorded 12% of the time on BBS routes in this region). Within this warmer area, the data were further partitioned by other variables into areas with higher and lower incidence of the bird. The left branch of the tree contained the cooler portions of the eastern United States, where the species had a high overall incidence (0.677) within this area. But within this branch, areas with high proportions of crop and pastureland (land cover class 1 as measured in the Anderson level II coverage of O'Connor et al. (1996) (lcc1.lco2 in Figure 2.2) right side of the split) largely lacked the species (mean inidence of 0.064). The left side of this split continued to branch in a complex manner, yielding 4 terminal nodes with higher incidence of the species. This model used eight different variables as predictors of the species occurrence in the eastern

Figure 2.2. Regression tree structure for the American redstart's conventional (A), GCM (B) and composite (C) models. The ellipses represent intermediate nodes in the regression tree, while the rectangles are terminal nodes. The numbers in the ellipses and rectangles give the predicted bird species incidence at each node. At each fork in the tree, the identity and value of the predictor variable involved is shown, and all cases in an end-node satisfy all the splitting criteria specified in traversing the tree from its root to that end-node. See Table 2.4 for a list of predictor variable abbreviations appearing here.




B)
0.200
JULT<21.00
JULT>21.00
0.832
0.114
lcc137<0.001
lcc137>0.001
lcc93<0.092
lcc93>0.092
0.321
0.750
0.086
0.310
lcc1.lco2<0.024
lcc1.lco2>0.024
ELV.CV<10.7
ELV.CV>10.7
lcc95<0.476
lcc95>0.476
lcc51<0.003
lcc51>0.003
0.509
0.112
0.571
0.824
0.073
0.350
0.522
0.182
JULT<23.87
JULT>23.87
ELV.CV<22.9
ELV.CV>22.9
0.555
0.120
0.122
0.400
C)
0.200
JIAvg<20.97
JIAvg>20.97
0.677
0.119
lcc1.lco2<0.569
lcc1.lco2>0.569
JIMn<20.5
JIMn>20.5
0.734
0.064
0.339
0.092
lccmax<0.839
lccmax>0.839
lcc7.lco2<0.732
lcc7.lco2>0.732
AvPS7.lco2<501.319
AvPS7.lco2>501.319
0.631
0.934
0.262
0.820
0.075
0.458
MIN.ELV<114
MIN.ELV>114
MIN.ELV<365.0
MIN.ELV>365.0
lcc52<0.033
lcc52>0.033
PET<87.72
PET>87.72
0.912
0.589
0.867
0.579
0.140
0.395
0.123
0.042
MIN.ELV<210.0
MIN.ELV>210.0
0.479
0.197

United States (Table 2.4, column 1). Average July temperature dominated the model, with minimum July temperature and crop and pastureland constituting the only other variables with R^2 greater then 5%.

When the GCM input climate variables and the landscape variables were used as potential predictors of the occurrence of American redstart, the root split occurred at an average July temperature of 21.08 °C (Figure 2.2B). The second variable on the left side of the root split was a land cover class namely northern mixed forest dominated by beech, birch, maple, spruce, fir and hemlock (land cover class 137 of Loveland et al. (1991)). On the right hand side of Figure 2.2B land cover class 93 - dominated by beech, birch, maple, oak, and pasture entered at the second split. Each of these variables explained more than 5% of the species deviance.

In comparing the GCM input and conventional models, it can be seen that the root node in both models involved average July temperature. However, the conventional and GCM input measures of July temperature are not identical because of the aggregation influence of cross-walking on the conventional measure. The difference in these two measures was large enough to allow for distinct daughter nodes to occur, such that 81 counties (3.8% of the total counties) were classified differently in each model at the average July temperature of 21 °C. Another difference between the conventional and GCM input species models (Figure 2.2A and B) is in the second split on the right side of these models, where the absence of a minimum July temperature variable in its input data forced the GCM input model to select a land cover variable. This omission implies that these two variables could be collinear in this portion in the eastern United States, but under perturbation both variables (July minimum and land cover class 93) remained

Table 2.4. Predictor variables that entered the three American redstart models with the conventional climate variables alone, with GCM climate variables alone, and with both types of climate variables present and the percent deviance in species occurrence explained by these variables. An asterisk denotes that the variable did not occur in the model.

Variables	Variable id	Conventional	GCM input	Composite
Average July temperature	JlAvg or JULT	47.2	47.2	47.2
July Minimum temperature	JlMn	8.4	*	8.4
Cropland and pasture, land cover class 1	lcc1.lco2	6.1	2.2	6.1
Deciduous forests, land cover class 7	lcc7.lco2	4.3	1.1	3.2
Minimum elevation	MIN.ELV	2.5	*	2.5
Average patch size of land cover class 7, Deciduous forests	AvPS7.lco2	2.5	*	2.5
Crop/woodland dominated by forage crops, hay, woodlots (land cover class 52)	lcc52	1.8	*	1.8
Maximum land cover occurrence	Lccmax	1.7	*	1.7
Northern mixed forest dominated by beech, birch, maple, spruce, fir, hemlock (land cover class 137)	lcc137	*	7.4	*
Northern deciduous forest dominated by beech, birch, maple, oak, and pasture (land cover class 93)	lcc93	*	5.7	*
Crop/woodland dominated by pasture, hay, corn, soybean, oak, hickory (land cover class 51)	lcc51	*	3.5	*
Elevation coefficient of variation	ELV.CV	*	3.0	*
Southern Deciduous forest dominated by oak, hickory, poplar, beech, and walnut (land cover class 95)	lcc95	*	3.0	*
Potential evapotranspiration	PET	*	*	1.4
Total R^2 (as percentage)		74.5	73.1	74.8

intact in their respective models, indicating the stability of these different variables in the two models. Despite these differences, the overall model performance was not affected (Table 2.4). For both models, the root split occurred at approximately the same temperature in both the conventional and GCM input species models. Similarly, both daughter splits (on the left side of each tree (Figure 2.2A, and Figure 2.2B)) used land cover class 1 (lcc1.lco2) > 0.57 and the presence of land cover class 137 of Loveland et al. (1991)(lcc137). These divisions identified very similar regions of the country (eastern Wisconsin and the Appalachian mountains in North Carolina and Virginia). Furthermore, average July temperature explained 47.2% of the species range in both the conventional and GCM input models.

The composite model was very similar to the conventional data one (Figure 2.2). The only difference was that potential evapotranspiration (PET), one of the GCM input variables, entered into the model and replaced the deciduous forest variable (land cover class 7 (lcc7.lco2)) in one position (Figure 2.2C). However, the incremental contribution of including both sets of climate variables was minimal; the GCM input variables added only negligibly (0.3) to the total model deviance explained (Table 2.4). Perturbation of the various variables in the three American redstart models yielded no evidence of collinearity problems. Average July temperature and minimum July temperature were highly correlated, but the substantive conclusion of the importance of July temperature in determining the occurrence of American redstarts does not change.

2.4.2 Summarized species model outcomes

The conventional, GCM input, and composite regression tree models of the seventeen species had total model R^2 values that ranged from 47.7 to 87.7% (Table 2.5),

Table 2.5. Total percent deviance explained (100*R^2) of each species for the conventional, GCM input and composite models.

	Conventional Models	GCM input Models	Composite Models
Eastern wood-pewee	59.6	47.7	52.3
Least flycatcher	72.2	69.5	72.2
Orchard oriole	77.1	75.9	76.6
Baltimore oriole	84.9	83.8	84.9
Field sparrow	70.5	73.3	74.2
Northern cardinal	87.7	87.6	87.7
Rose-breasted grosbeak	86.0	84.6	85.9
Dickcissel	81.1	82.7	82.3
Summer tanager	87.0	86.0	87.0
Magnolia warbler	80.5	77.0	80.7
Black-throated green warbler	79.1	74.2	79.4
Pine warbler	78.8	80.5	80.8
Prairie warbler	73.7	67.4	73.2
American redstart	74.5	73.1	74.8
Gray catbird	77.8	78.0	77.8
Brown thrasher	66.6	68.0	62.4
Blue-gray gnatcatcher	74.1	73.7	73.2
Mean	**77.1**	**75.5**	**76.8**

and there was considerable agreement in the three sets of models of each species. In fact, the within species differences in total R^2 between conventional and GCM input models averaged only 1.7 (± 3.2 SD) percentage points and was not statistically different when tested with a Wilcoxon Signed Ranks test ($P > 0.05$). These small differences between species models resulted in a strong positive relationship across all of the species for the two sets of models ($r_s=0.94, r_{s0.05(2)17}=0.485, P<0.001$).

Climate variables clearly dominated all the models (Figure 2.3). In the conventional models they contributed on average 57.5 percentage points to the mean R^2 (across all seventeen species) of 77.1% (±7.5 SD); in the GCM input models they contributed an average of 53.6 percentage points to the mean R^2 of 75.5% (± 9.1 SD); and in the composite model they contributed 57.7 percentage points to the average of 76.8% (± 9.0 SD). The slightly lower predictive power of the GCM input climate data suggests by these figures appears to be present: in 13 of the 17 species the climate variables made more of a contribution in the conventional than in the GCM input models (Wilcoxon Signed Ranks test, $P<0.025$). In addition, within the composite models much of the climate contribution came from the conventional rather than from the GCM input variables (Figure 2.4).

When each of the climate variables in the seventeen species composite models was perturbed by 5% and the model re-run, the mean change in total model R^2 was only 0.44 (± 0.85 SD) percentage points. This small change in the species models indicated that the models were robust. Furthermore, in the eleven species models in which the perturbed conventional climate variables were replaced by GCM input variables, the a mean change in R^2 was only 0.22 (± 0.66 SD) of a percentage point. These small

Figure 2.3. Frequency distribution of the contributions (measured as percent deviance explained) of climate variables and land cover variables in the conventional (A, B), GCM input (C, D) and composite (E, F) models for the 17 bird species.

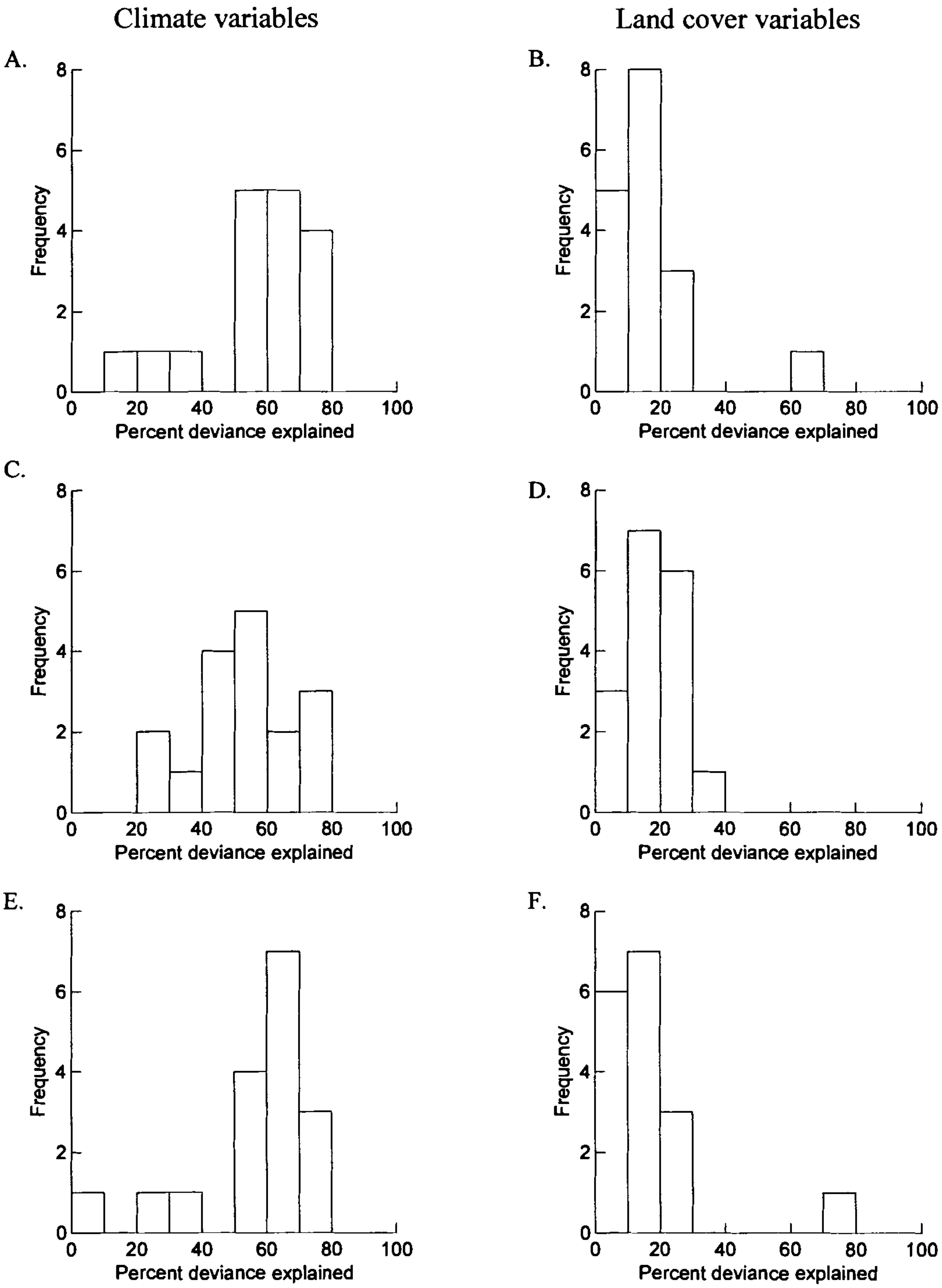
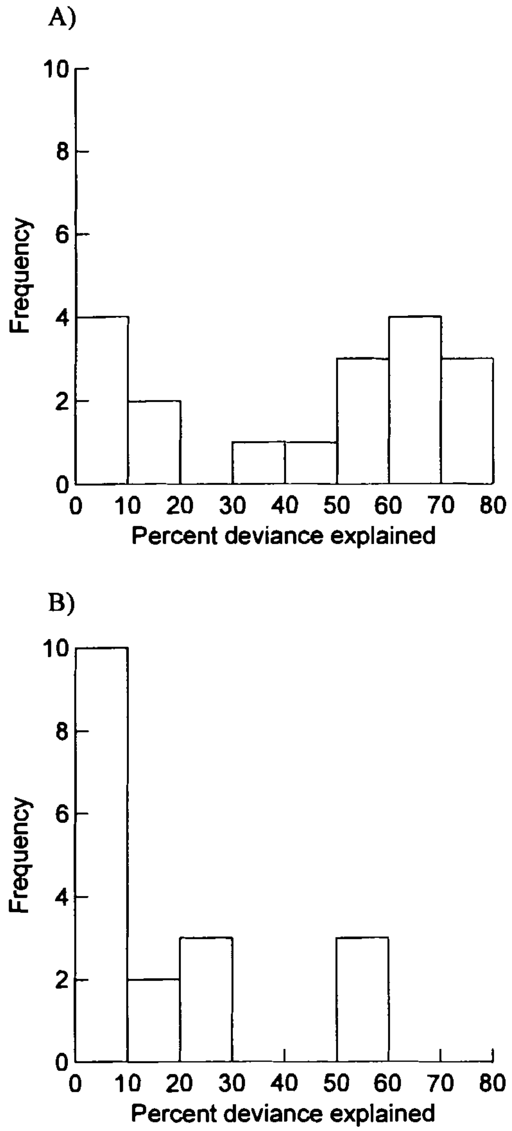


Figure 2.4. Frequency distribution of the relative contribution to the composite species models (N = 17) of A) conventional climate variables and B) GCM input climate variables. Relative contribution is expressed as percentage of the species deviance explained.



changes indicated that the GCM input data were effective replacements for the conventional climate data.

2.5 Discussion

The basis for any projection of a species distribution onto climate change scenarios is the ability to create a representative model of the current distribution. In this analysis there is clear evidence that the climate variables available as GCM outputs can be used to construct representative models of species distributions, as long as land cover and elevation variables are also included as potential predictors. There was a significant positive correlation between the overall goodness-of-fit for GCM input and conventional models. Nor were there significant differences in the total model predictability among the tree classes of models considered: the within species differences averaged only 1.7 (± 3.2 SD) percentage points between the conventional and GCM input models, 1.3 (± 2.6 SD) points between the GCM input and composite models, and 0.4 (± 2.4 SD) points between the conventional and composite models. Use of the GCM input climate data sets thus resulted in little loss in model explanatory power.

Many studies have documented the importance of climate variables for modeling vertebrate species distributions and richness at regional scales (Caughley et al. 1987, Currie 1991,O'Connor et al. 1996, and Root 1988a). Correspondingly, there was a clear dominance of these variables in the seventeen models at the U.S. county grain presented here (Figure 2.3). The significance of climate variables for coarse resolution modeling of bird distributions underscores the importance of the present evaluation of common GCM climate metrics, as they will play essential roles in describing species distributions responses to climate change. Furthermore, based on the evidence from this analysis, variables that describe variation in the distributions of forests and elevation were also important components of all the species models. While these vegetation and elevation variables contributed less in overall magnitude to the total R^2 of the models, they still contributed important patterns of the species distributions.

These non-climate variables, were also particularly important in complementing the lower predictive power of the GCM variables. The presence and relative importance of climate variables in the models run with GCM input variables was less than in the models with the conventional climate data. The GCM climate variables were therefore not completely analogous to the conventional climate variables in their ability to describe species distributions. Despite this, the models did not differ in their ability to represent the species distributions. The vegetation and elevation variables were therefore important contributors to the species models, as they were able to make up for any differences between the two climate data sets in the modeling process.

In the case of the composite models where the two climate data sets were in direct competition with each other, the conventional variables clearly contributed more to the total explanatory ability of the composite models than did the GCM input variables (Figure 2.4). However, under 5% perturbation GCM input variables readily replaced conventional variables in the regression trees, with only minor loss in the model's explanatory ability. This finding implies that the GCM input variables were adequate though slightly inferior surrogates for the conventional climate variables.

The weaker performance of GCM input climate variables could in part be explained by their original purpose. GCMs attempt to model the complex interactions of physical processes across the Earth in order to gain an understanding of climate patterns (Root and Schneider 2002). The resolution must be coarse in order to smooth out underlying variability. As a result, the types of outputs are typically broad classifications of long-term climate conditions intended to facilitate comparisons with current climate patterns rather than with biogeographic data. Conversely, the climate variables of the conventional data set were collected with the prior knowledge that they show associations with the distributional patterns of birds. At the same time, though, there was considerable agreement between the two sets of climate variables in this study (Table 2.2). In particular, the complex of climate variables can be described by two different sources of variation across the extent of the study: a north-south and an east-west gradient. This suggests that the importance of climate conditions on birds (Ashmole 1963, Root 1988a, Currie 1991, and O'Connor et al. 1996) can be captured in these two sources of variation across the eastern U.S., and given the high loadings of the GCM input variables along these two gradients appear to adequately characterize these dominant climate patterns. The influence of long term seasonal averages (seasonality and yearly average temperatures) and winter temperatures (January temperature) (the first component in Figure 2.1A) highlight the north-south patterns of species richness and distributions identified by previous studies (Ashmole 1963, Root 1988a, and O'Connor et al. 1996). The second component was largely defined by July temperatures and evapotranspiration (PET), described by Currie (1991) to be important influences on species' productivity. The influence of PET is especially worth noting and should be included in future studies of species occurrence as it contributes greatly to an unique axis of climate variation in the eastern United States.

The comparison of the performance of conventional and GCM climate data were evaluated here exclusively in the context of regression tree models. A wide variety of statistical procedures are available to construct models of the species' distributions and might yield different weaknesses about the value of GCM variables. However, De'ath and Fabricius (2000) reported that regression trees outperformed linear methods such as forward and backward stepwise regression in describing the abundance of soft coral taxa. Likewise, Rejwan et al. (1999) found that models created with regression trees were both more accurate and more precise in describing nesting sites of smallmouth bass than models created with standard multiple regression. Furthermore, regression trees are able to relax the strict linear constraints that are required by other multivariate modeling procedures (Clark and Pregibon 1992). Iverson and Prasad (1998) noted the method's ability to handle interactions between independent variables without the need to identify the interactions a priori. Therefore, the flexibility and performance of regression tree analysis is very well suited to the complex nature of modeling bird species occurrences across large extents, particularly to our ability to model species redistribution patterns based on GCM scenarios. Under current conditions, the types of climate variables that are commonly obtained from GCMs, although not exact replacements of conventional climate data, perform well in modeling bird distributions in the eastern United States. The present study therefore provides a validation of the utility of GCM climate variables as inputs to models of biotic distributions.

Chapter 3

REDISTRIBUTION OF BIRD SPECIES IN THE EASTERN UNITED STATES UNDER CLIMATE CHANGE SCENARIOS

3.1 Abstract

With mounting evidence that global temperatures have increased significantly over the last century and with projections of even greater changes in climate by the end of this century, understanding the potential consequences of climate change for species distributions is essential to conservation efforts. Here, I evaluated the potential response of 152 bird species in the eastern United States to projected climate change. By projecting both where suitable climate conditions will occur, and what types of vegetation will be available at each location, I obtained a more comprehensive understandingof likely future distribution of birds thanwas possible in previous studies of the biotic consequences of climate change for birds.

Using regression tree analysis, I produced models of current bird species abundance for all counties east of the 100th meridian. The potential predictors of the species included 8 climate, 4 elevation, and 80 individual tree species abundance variables. The regression tree modeling produced for each species a set of decision rules based on a species-specific subset of these environmental. Species models were considered acceptable only if they accounted for at least 50% of the deviance in abundance and in practice ranged in total R^2 from 50.9-91.0%, with an average R^2 = 73.3%; average classification accuracy was75.6%. The spectrum of predictor variables that occurred in the species models ranged widely, but only one of the species models was comprised solely of climate variables. This finding indicates the importance of

including both climate and landscape variables in creating representative species models at this resolution.

The decision rules of these models were applied to the projections of future climate distributions generated by two General Circulation Models (GCMs), one the Canadian Climate Center (CCC) model, the other the Hadley Center for Climate Prediction and Research (Hadley) model; both are scenarios of global climate change with an equilibrium doubling of atmospheric CO_2 concentrations. Under the CCC and Hadley scenarios, theeastern U.S. populations of 78 and 71 species respectively were projected to decrease by at least 25%, while the populations of 37 and 30 species were projected to increase by at least 25% within the eastern United States. The projected changes in the species range were similarly dramatic, with 59 and 53 species respectively projected to decreasetheir eastern U.S. range by at least 25%, andwith 34 and 25 speciesprojected to increase by at least 25%.

Species models that contained a high proportion of vegetation variables in their models had a high percentage of the projected losses in species distributions, while species models that were dominated by climate variables showed approximately equal percentages of gains and losses in their distributions. This suggests that species associated with vegetation variables may be restricted by a smaller area of suitable habitat then those species that showed stronger associations with broader patterns of climate variation. The results from this analysis suggest that under these two scenarios of global climate change the potential consequences to bird species populations and communities in the eastern United States would be substantial.

3.2 Introduction

There is mounting evidence that current global climate is changing due to increased concentrations of greenhouse gases in the earth's atmosphere (IPCC 2001). These substantial increases in greenhouse gases, which are attributed to human activities, are projected to continue, contributing to further global climate change. While the climate has constantly changed through time, the projected rate of climate change is steeper than at any other time over the last 1000 years. There is mounting evidence that species have already begun to respond to global climate change (Parmesan et al. 1999, Thomas and Lennon 1999, Walther et al. 2002, Moss et al. 2001), a trend that is likely to intensify with accelerating changes in climate. Evaluation of the potential consequences of continued global climate change on flora and fauna is of high interest to conservation efforts and to natural resource management (Kareiva et al. 1993).

General Circulation Models (GCM) have been used to explore how the climate on earth might change under increased concentration of greenhouse gases. The goal of a GCM is to model physical climate processes across the earth (Baede et al. 2001), based on current understanding of the complex interactions among the physical processes that influence climate conditions (Gates 1993). Since their origination, the development of GCMs has been rapid and efficient, and they now allow for confident predictions of climate patterns at coarse spatial resolution (Albritton et al. 2001). Under various GCM scenarios of doubling CO_2 in the atmosphere, the earth's global mean temperature is projected to increase between 2 and 6 degrees Celsius by the end of the 21st century (IPCC 2001).

The projected rapid shift in temperature is expected to impose considerable constraints on many species (Kareiva et al. 1993). For birds, patterns of breeding species richness in the United States reflect the importance of climate (Ashmole 1963, Currie 1991). However, Root (1988b) identified associations between minimum winter temperatures and important metabolic constraints of individual bird species that drive some species' northern winter distributional limit. Thus, correlations between various climate variables and bird distributions provide a fruitful avenue to explore the potential responses of birds to climate change. In fact, relationships between climate and birds were used to project future bird species ranges in North America (Sorenson et al. 1998, Price and Root 2001, Price and Glick 2002) and South Africa (Erasmus et al. 2002) under various climate change scenarios.

However, birds are not constrained solely by climate variables. Even at large spatial extents other factors, such as vegetation distribution, are important components in shaping species abundance patterns. A comprehensive understanding of how bird species might respond to predicted temperature changes requires a consideration of these factors as well. Projected shifts in vegetation patterns in response to global climate change have in fact been the focus of much research (Hansen et al 2001, Iverson and Prasad 1998). In the past, tree species moved independently of each other, leading to considerable changes in tree communities over time (Jacobson et al. 1987, Clark 1993), a dynamic that we should expect to continue in the future. Iverson and Prasad (1998) predicted the future distributions of 80 major tree species in the eastern United States, and the availability of their vegetation projections allows a more complete understanding of the potential movements of birds in response to global climate change.

The focus of this chapter is to assess the potential consequences of global climate change for individual bird species distributions in the eastern Unites States. Projections of this type represent the potential envelope of suitable conditions for the species based on the predictor variables and are accurate forecasts offuture distributions only to the extent that these response-predictor relationships remain unchanged. Should the birds adapt to the changes in climate, future distributions will be different. It is also important to recognize the importance of interspecific competition in shaping species abundance patterns across their range and its significance to the potential movements of species in response to climate change (Davis et al. 1998). The present analysis, therefore, provides projections of future bird distribution that incorporates current understanding of both future climate variables and future tree distributions as primary determinants of distribution, to gain a broad perspective on the potential response of bird species populations under two scenarios of climate change. It does not assess the secondary effects of changed competitive environments resulting from shifts in the ranges of competing species or from adaptive responses by birds to their changed circumstances.

3.3 Methods

The study area encompassed the United States east of the 100th meridian and was analyzed at the resolution (grain size) of United States counties. This extent and grain matched those used by Iverson and Prasad (1998), the work on which the predictor variables in this analysis were based. Although counties are not equal in size across the coterminous United States, which could induce errors from variable sized sample units, this analysis was restricted to counties east of the 100th meridian, which are relatively similar in size (Iverson and Prasad 1998).

3.3.1 Bird data

The data for 186 individual bird species of the eastern US came from the national Breeding Bird Survey (BBS) for the years of 1981 and 1990. O'Connor et al. (1996) extracted 1223 high quality routes across the conterminous United States and matched these routes tocells of the EMAP 640 km^2 hexagonal grid of White et al. (1992). These routes were representative of all land cover in the conterminous U.S., except that high elevation land is somewhat under-represented (J.J. Lawler and R.J O'Connor unpublished data). Yang et al. (1995) interpolated the species incidences for each species to obtain a complete coverage abundance surface across the conterminous United States at the hexagon resolution.

However, the climateand tree projectionsdeveloped by Iverson and Prasad (1998) were only available for counties, so I cross-walked the bird data from hexagons to counties. I created unique polygons by overlaying hexagons and counties and matched them to hexagons through their associated county identification. The bird species incidences from the hexagons were assigned to the appropriate polygons and these polygons were area-weighted within each county to arrive at an estimate of the bird species incidence in each county (Matthews et al. 2002).

3.3.2 Predictor variables

The independent variables that were used as potential predictors of the bird species occurrence were obtained from Iverson and Prasad (1998). These variables consisted of eight climate variables (average yearly temperature, average July temperatures, average January temperatures, average precipitation, seasonality (measured as the difference between average July and January temperature), potential evapotranspiration, average May to September temperature, and drought stress (measured as July-August ratio of precipitation to potential evapotranspiration). The minimum, maximum, and coefficient of variation of elevation were also included as potential predictors variables. I also calculated the mid-range of the maximum and minimum elevation in each county to arrive at an estimate of the average elevation in the county. Finally, tree species importance values (a measure of abundance) for eighty species, derived from Forest Inventory Analysis data and aggregated to the county resolution by Iverson and Prasad (1998), were added. These potential predictors provide a wide array of predictor variables that a priori evidence indicated might be associated with bird species abundance patterns.

3.3.3 Statistical analysis

Regression tree models (Breiman et al. 1984, Clark and Pregibon 1992) for the individual bird species were created from the above suite of environmental variables, using the regression tree software in S-Plus version 6 (Insightful 2001). This method was chosen as it has many advantages over traditional methods of regression that rely on linear relationships for identifying associations between independent and dependent variables. First, regression trees can accommodate non-linear relationships among dependent and independent variables, and are less sensitive to outliers (Verbyla 1987). Second, the method is able to handle interactions between independent variables by sub-setting the data in the tree building process without the need to identify all possible interactions a priori. Third, despite the less restrictive assumptions of regression trees, they have been shown to be as efficient, and in some cases better than, the more traditional method of multiple regression (De'ath and Fabricius 2000, Rejwan et al. 1999).

The regression tree algorithm orders the sample by the values of each predictor variable, in turn, and searches through all possible binary splits of the data along the resulting gradient. It accepts the split at the point at which the predictor maximizes the differencebetween the two subsets in the deviance in the dependent variable (in this case the species abundance). This process continues independently and recursively on each of the two sub-sets formed until pre-selected stopping criteria are reached. The model obtained from the initial growth is typically over-fit and measures must be taken to reduce the number of variables and splits (Breiman et al. 1984, Clark and Pregibon 1992,Venables and Ripley 1994). To this end, I conducted ten-fold cross-validation procedures to determine the optimal number of terminal nodes and pruned back the trees to these number nodes. If any of the remaining variables explained less than 1% of the deviance in the species data it also was removed. This procedure served to eliminate a slight bias in the S-Plus default cross-validation towards accepting slightly over-large trees (J. Sifneos unpublished data). Once I had created and validated the final regression tree model, I calculated the proportion of the deviance in the species data that were associated with each variable in the model as a measure of the mean deviance explained, representing this as a $100*R^2$ value.

In addition to the R^2 values calculated for each of the models, a comparison was made between the original data and the predicted model. To obtain a metric of how well the species models reconstructed the original species distribution, the classification accuracy was calculated according to Iverson and Prasad (1998) as:

$$C = \left(\frac{b}{b + x + z} \right) \times 100 ,$$

where C is the percentage classification accuracy; b is the number of counties in which the species was predicted according to the model and actually present; x is the number of counties in which the species was present but not predicted; and z is the number of counties where the species was predicted but not present. Species were considered to be absent (for predicted and original incidences) if their incidence was less than 0.05. This minimum incidence value was set to prevent a potential overestimation of the range, which might have occurred as a consequence of cross-walking from the original 640 km^2 hexagons to counties.

3.3.4 Future bird species abundance

The projected future climate data come from the Canadian Climate Centre (CCC) model (Boer et al. 2000, and Kittel et al. 2000) and the Hadley Center for Climate Prediction and Research (Hadley) model (Mitchell et al., 1995). Both models project the climate based on an equilibrium doubling of CO_2 from its 1994 level, which is anticipated to be reached by the end of the 21st century. These two scenarios are essentially the extremes of the available GCM predictions: the CCC scenario projects more severe changes in temperature, while the Hadley scenario projects milder temperature changes, but greater increase in precipitation across the eastern U.S.

I obtained predicted future distributions of 80 tree species from Prasad and Iverson (1999) Future tree distributions are not determined solely by the future locations of suitable climate since trees must be able to reach these areas through dispersal. Iverson and Prasad (1999) therefore determined these future distributions by intersecting maps of the dispersal potential of each species onto their climate envelope.

I then used the decision rules of the contemporary bird distribution models to predict future bird distributions based onthe projected climate and tree distributions. From these projections, I quantified the population consequences of climate change for each bird species in the eastern United States, using an area-weighted change in species occurrence. This metric was calculated as:

$$P = \left[\frac{\sum_i \left(w_i (a_i - b_i) \right)}{\sum_i w_i a_i} \right] \times 100,$$

where P is the percentage change in species population; i is the county identifier; w is the weighted area of the county in the study area; a is the present species incidence ranging from 0-1, and b is the predicted species incidence under the GCM scenario.

I also quantified the overall change in the species eastern range as:

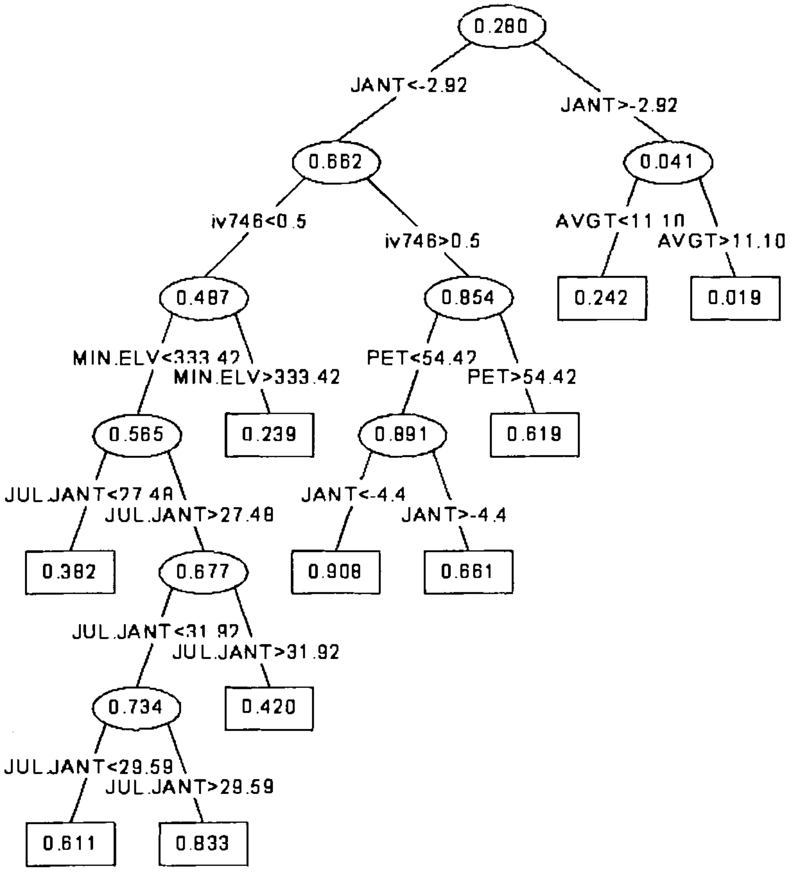
$$R = \left(\frac{f - c}{c} \right) \times 100,$$

where R is the percentage change in the species distribution; f is the area of the predicted range; and c is the area of the current range.

3.4 Results

Regression tree models weresuccessfully developed and cross-validated foran initial 186 bird species across the eastern United States. To illustrate the output of these regression tree models, I present the results of the rose-breasted grosbeak(*Pheucticus ludovicianus*) as an example (Figure 3.1). Average January temperature produced the first binary partition in the rose-breasted grosbeak model, at the threshold of –2.92 °C. The left branch identified colder areas of the species range and indicated an average incidence of 0.66 (i.e., the species was recorded 66% of the time on the BBS routes in

Figure 3.1. Regression tree structure form the rose-breasted grosbeak. The ellipses represent intermediate nodes in the regression tree, while the rectangles are the terminal nodes. For each internal node the regression tree shows the threshold split variable and value. The numbers in the ellipses and rectangles give the predicted bird species incidences at that point. AVGT is the average yearly temperature (°C); iv746 represents the abundance of Quaking aspen (Populus tremuloides); JANT is the mean January temperature (°C); JUL.JANT is the difference between July and January mean temperature(°C); MIN.ELV is the minimum elevation (m); PET is Potential evapotranspiration.



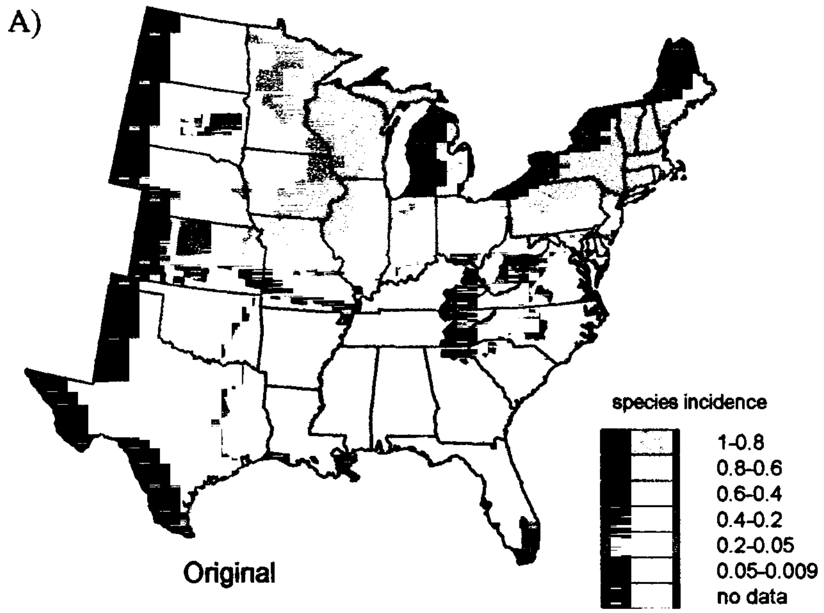
this temperature zone), while the right branch encompassed the warmer portions of the eastern United States, and had a very low average incidence of the species (0.04). The left branch of the tree (i.e., areas with average January temperatures below –2.92 °C) was split next by the abundance of quaking aspen, with areas containing greater abundance of aspen having a higher average bird species incidence. The regression tree continued to branch in this manner until terminal nodes were reached, at which point counties that met all the thresholds characteristics of an end node in this model were predicted to have the average rose-breasted grosbeak incidence of that end node (Figure 3.1). There were six different variables in the grosbeak's model, with January temperature contributing 67.0 percentage points to the total model R^2 of 86.3 (Table 3.1). I used these decision rules from the model to predict the rose-breasted grosbeak's current abundance (Figure 3.2). Similarly, models for the other 185 bird species provided distribution and abundance predictions based on the environmental determinants that occurred in the individual models.

Good model fit under present environmental conditions was a prerequisite for a successful projection on future conditions. I used both the total R^2 of a model, which represents how well a model partitions the occurrence of a species, and the classification accuracy, which provides information on how well the modeled distribution recreates the original species distribution, as measures of goodness-of-fit (Figure 3.3). Quantile plots of the classification accuracy and total R^2 for the 186 species showed tailed distributions and distinct breaks in the distribution when each measure fell below 50% (Figure 3.4). This process enabled me to evaluate the results of the species models and to identify four groups of species that had different model performance (Figure 3.3). Fifteen models had

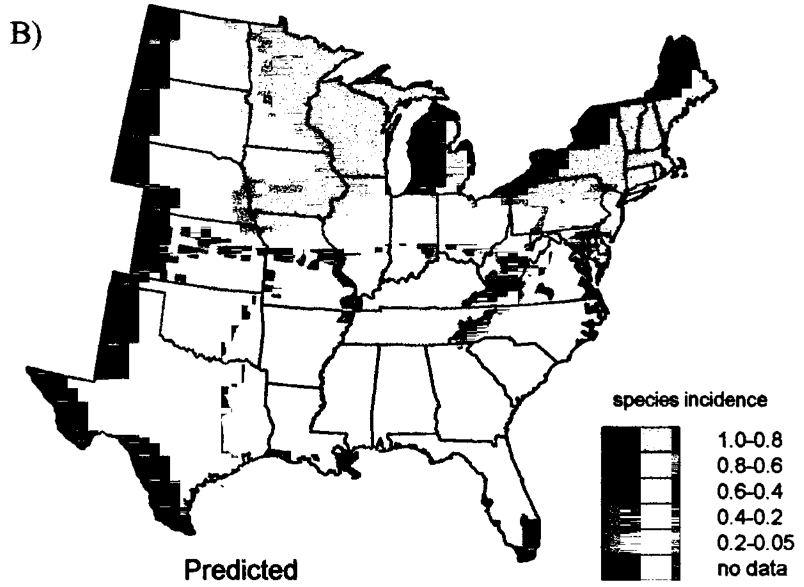
Table 3.1. Predictor variables that entered the rose-breasted grosbeak models and the percent deviance in species occurrence explained by these variables.

Variable names	Variable ID.	R^2
Mean January temp	JANT	67.0
Populus tremuloides	iv746	9.4
Difference in July and January temp	JUL.JANT	4.0
Minimum elevation	MIN.ELV	2.8
Mean annual temp	AVGT	1.9
Potential evapotranspiration	PET	1.2
Total R^2		86.3

Figure 3.2. Map of the rose-breasted grosbeak's current species distribution as determined by BBS data (A), and as predicted by the species' regression tree model (B).



Original



Predicted

Figure 3.3. The classification accuracy of the 186 species models in relation to the corresponding model total R^2. The dots represent species models with both total R^2 and classification greater than 50%. The crosses represent species model with both classification accuracy and total R^2 below 50%. Squares represent species models with total R^2 below 50% but classification accuracy above 50%. Triangles represent models with total R^2 above 50 % and classification accuracy below 50%.

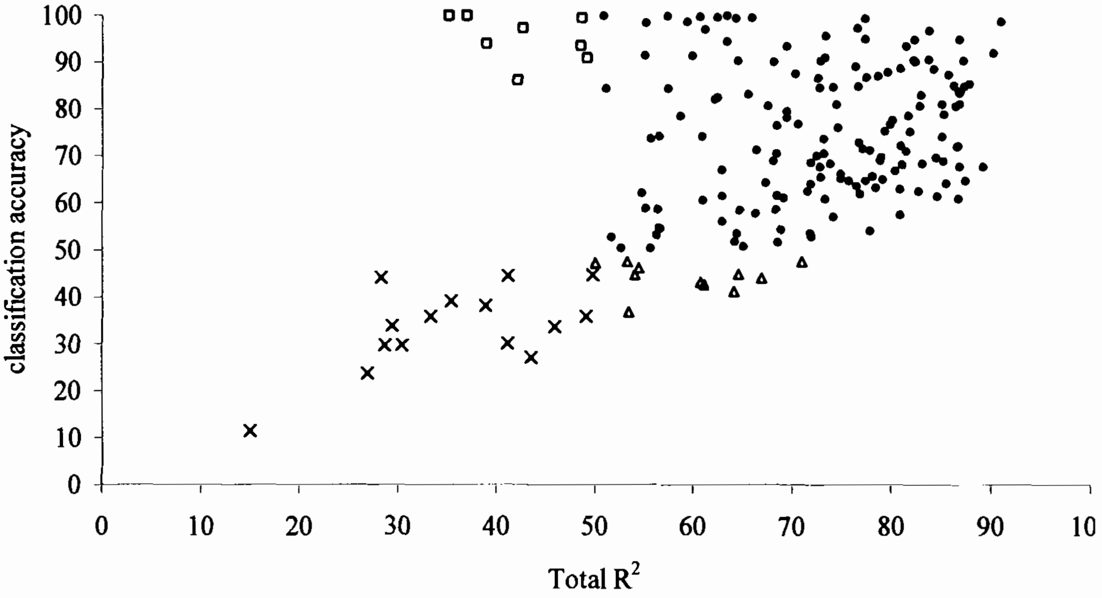
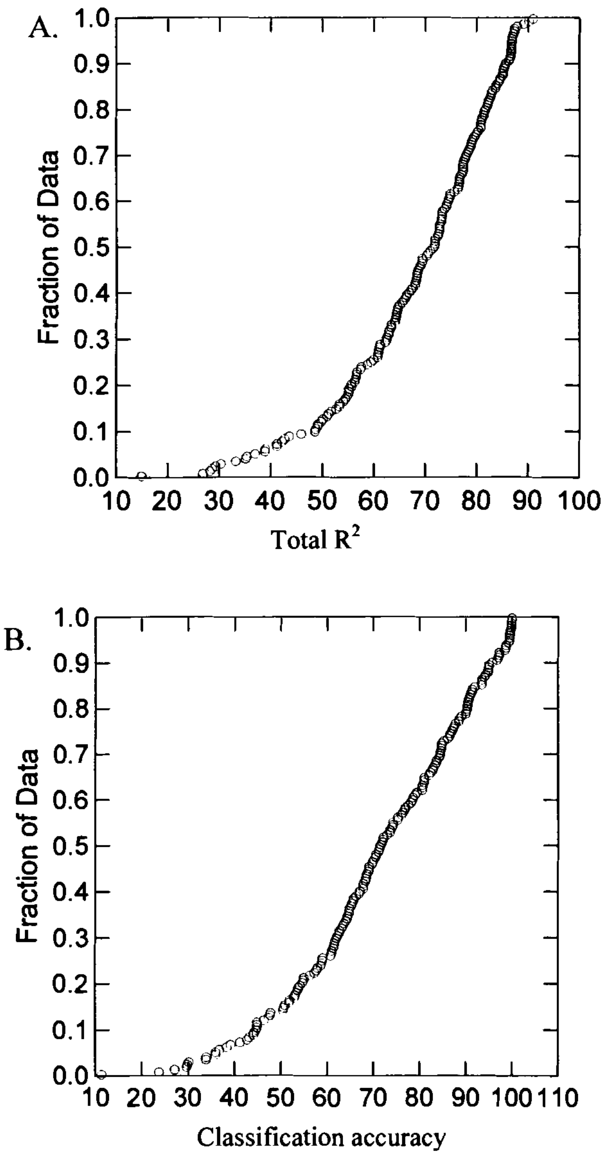


Figure 3.4. Quantile plots for the total R^2 (A) and the classification accuracy (B) of the 186 species models.



classification accuracy and total R^2 below 50%, and correspond to the long tail in Figure 3.3. The species contained in this group yielded the poorest models. An example of a species in this group was the sharp-shinned hawk (*Accipiter striatus*) (Figure 3.5 A and B). Eleven species had models with a total R^2 greater than 50% but classification accuracy below this threshold value (see the herring gull (*Larus argentatus*) in Figure 3.5 C and D as an example of this type of species). Even though more than 50% of the species variation across the eastern United State was captured in these models, they correctly classified less than half of the counties that the species currently occupied. Next, there were eight species that had a classification accuracy above 50 % but a total R^2 below 50%. These species had very large ranges across the eastern United States, so that a correct classification was easily achieved, but the models were unable to accurately describe the species' variation in occurrence within this range. The map for the yellow-throated vireo (*Vireo flavifrons*) (Figure 3.5 E and F) illustrates this class of species.

The performance of current distribution models of the 34 species comprising these three groups was deemed unacceptable for projecting the species distributions onto future climate scenarios. On the other hand, the remaining group of 152 species produced models that adequately depicted the species current abundance (an example being the rose-breasted grosbeak Figure 3.2), and thus were suitable to project onto the CCC and Hadley climate change scenarios.

I then projected theses species on to the two climate change scenarios, and compiled the difference between the species' current and potential future distributions for each county. I found that the predicted changes in bird population and range varied greatly among species, both for the CCC and for the Hadley scenarios (Table 3.2).

Figure 3.5. Map of the current species distribution for the BBS data (A,C,E) and for the predicted distribution produced by the regression tree model (B,D,F) for the sharp-shinned hawk (A and B), herring gull (C and D), and yellow-throated vireo(E and F).

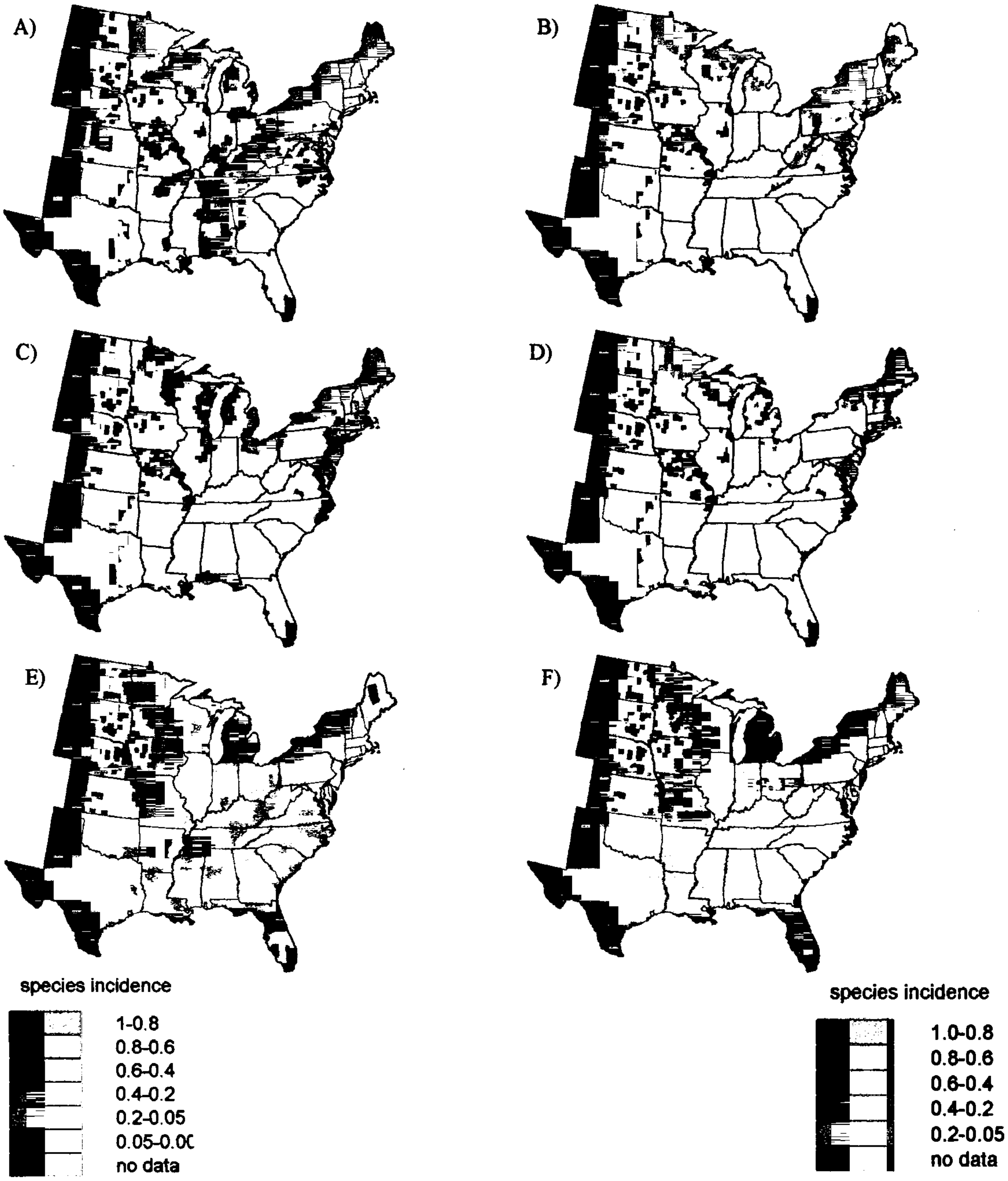


Table 3.2. Total R^2 of the regression tree model for each species under current conditions, and the relative contribution of climate variables in the model (sum of climate variables R^2/Total R^2), along with the potential changes in bird species populations and ranges in the eastern United States for the CCC and Hadley GCM scenarios.

Species	Total R^2	Rel. Climate variables	CCC		Hadley	
			Population	Range	Population	Range
Common Loon (Gavia immer)	73.8	25.3	-100.0	-100.0	-90.1	-85.8
Ring-billed Gull (Larus delawarensis)	52.7	65.1	-99.6	-99.3	-64.8	-54.0
Laughing Gull (Larus atricilla)	68.9	30.9	-53.2	0.0	-40.3	0.0
Black Tern (Chlidonias niger)	75.7	12.2	-100.0	-100.0	-81.9	-69.2
Mallard (Anas platyrhynchos)	71.5	69.9	-53.5	0.0	-33.4	0.0
Blue-winged Teal (Anas discors)	82.7	11.3	-72.3	-51.2	-74.3	-63.8
Canada Goose (Branta canadensis)	56.4	50.9	-63.2	-43.3	-42.1	-42.2
White Ibis (Eudocimus albus)	79.3	76.4	145.4	150.6	23.3	23.6
American Bittern (Botaurus lentiginosus)	72.8	72.4	-100.0	-100.0	-84.6	-76.1
Great Blue Heron (Ardea herodias)	55.1	41.0	2.4	0.0	-11.8	0.0
Great Egret (Ardea alba)	74.9	72.9	122.6	173.7	49.4	74.5
Snowy Egret (Egretta thula)	63.0	31.9	118.7	251.9	70.0	123.2
Little Blue Heron (Egretta caerulea)	77.1	91.3	136.5	120.1	62.7	54.6
Cattle Egret (Bubulcus ibis)	85.1	96.2	197.9	152.1	86.6	75.2
Green Heron (Butorides virescens)	63.4	76.7	22.2	0.0	19.2	0.0
Yellow-crowned Night-Heron (Nyctanassa violacea)	68.4	58.8	178.8	161.5	60.2	85.7
Sora (Porzana carolina)	77.9	0.0	-100.0	-100.0	-95.8	-92.7
American Coot (Fulica americana)	71.9	4.1	-100.0	-100.0	-95.3	-87.4
Common Snipe (Gallinago gallinago)	77.8	86.4	-100.0	-100.0	-86.2	-72.5
Spotted Sandpiper (Actitis macularia)	54.8	64.9	-79.3	-76.3	-65.9	-47.3
Killdeer (Charadrius vociferus)	65.9	8.9	4.2	0.0	4.1	0.0
Gray Partridge (Perdix perdix)	84.6	39.3	-99.3	-98.8	-81.1	-67.0
Northern Bobwhite (Colinus virginianus)	82.3	94.3	49.0	31.1	26.8	19.3
Ruffed Grouse (Bonasa umbellus)	60.9	16.4	-84.5	-70.0	-63.7	-46.0
Ring-necked Pheasant (Phasianus colchicus)	82.9	97.2	-30.6	-38.1	-14.7	-20.8
Rock Dove (Columba livia)	61.2	24.5	-30.6	0.0	-12.7	0.0
Mourning Dove (Zenaida macroura)	63.4	0.0	2.5	0.0	2.2	0.0
Common Ground-Dove (Columbina passerina)	85.2	3.7	10.3	229.9	-61.9	48.4
Turkey Vulture (Cathartes aura)	64.5	72.4	84.8	11.6	35.7	8.6
Black Vulture (Coragyps atratus)	73.2	96.4	201.0	84.4	76.6	24.8
Mississippi Kite (Ictinia mississippiensis)	56.3	62.9	213.3	224.1	300.3	328.6
Northern Harrier (Circus cyaneus)	68.3	24.4	-41.9	-0.6	-54.4	-26.2
Red-tailed Hawk (Buteo jamaicensis)	55.2	41.6	31.0	0.0	31.2	0.0
Red-shouldered Hawk (Buteo lineatus)	74.6	88.9	64.7	42.9	10.7	7.5
Swainson's Hawk (Buteo swainsoni)	74.9	89.3	827.1	1042.9	811.1	1024.9
Broad-winged Hawk (Buteo platypterus)	56.6	12.2	-19.8	1.0	18.6	18.6

Table 3.2 continued

Species	Total R^2	Rel. Climate variables	CCC		Hadley	
			Population	Range	Population	Range
American Kestrel (Falco sparverius)	70.3	14.0	-16.1	-5.7	-7.1	-0.9
Great Horned Owl (Bubo virginianus)	55.7	30.8	3.5	0.0	5.8	0.0
Yellow-billed Cuckoo (Coccyzus americanus)	83.8	94.6	35.5	0.0	22.1	0.0
Black-billed Cuckoo (Coccyzus erythropthalmus)	77.5	96.7	-71.8	-57.1	-38.1	-23.1
Yellow-bellied Sapsucker (Sphyrapicus varius)	81.0	0.0	-100.0	-100.0	-63.0	-60.3
Pileated Woodpecker (Dryocopuc pileatus)	70.6	69.9	23.2	0.0	5.0	0.0
Red-headed Woodpecker (Melanerpes erythrocephalus)	74.2	8.1	3.6	0.0	25.2	0.0
Red-bellied Woodpecker (Melanerpes carolinus)	80.9	74.0	29.0	0.0	16.2	0.0
Chuck-Will's Widow (Caprimulgus carolinenis)	74.5	88.4	98.3	70.4	32.0	33.9
Whip-poor-will (Caprimulgus vociferus)	55.2	33.1	-38.2	6.3	-12.2	21.5
Common Nighthawk (Chordeiles minor)	56.7	72.4	127.8	0.0	108.1	0.0
Chimney Swift (Chaetura pelagica)	59.4	92.5	-1.5	0.0	0.5	0.0
Ruby-throated Hummingbird (Archilochus colubris)	59.9	28.9	13.0	14.7	6.5	15.6
Scissor-tailed Flycatcher (Tyrannus forficatus)	71.9	59.6	515.7	540.7	298.8	396.1
Eastern Kingbird (Tyrannus tyrannus)	62.5	39.0	12.7	2.0	40.7	2.0
Western Kingbird (Tyrannus verticalis)	76.8	82.4	27.6	-4.6	-4.5	-12.7
Eastern Phoebe (Sayornis phoebe)	62.9	34.5	5.5	0.0	12.9	0.0
Eastern Wood-Pewee (Contopus virens)	58.7	26.3	5.9	0.0	24.9	0.0
Acadian Flycatcher (Empidonax virescens)	68.1	69.3	-13.7	43.1	-16.1	25.2
Willow Flycatcher (Empidonax traillii)	56.6	41.7	-78.7	-63.6	-36.0	-21.0
Least Flycatcher (Empidonax minimus)	72.0	7.9	-98.5	-95.5	-67.2	-56.2
Horned Lark (Eremophila alpestris)	68.4	14.5	-36.0	-24.5	-36.2	-24.5
Blue Jay (Cyanocitta cristata)	57.5	44.8	-39.1	0.0	-28.0	0.0
American Crow (Corvus brachyrhynchos)	51.2	36.5	-42.3	0.0	-26.5	0.0
Fish Crow (Corvus ossifragus)	74.2	77.3	66.8	13.0	33.4	3.6
European Starling (Sturnus vulgaris)	50.9	64.6	-4.0	0.0	-6.5	0.0
Bobolink (Dolichonyx oryzivorus)	86.8	100.0	-86.0	-74.7	-41.6	-29.4
Brown-headed Cowbird (Molothrus ater)	64.3	68.7	-5.9	0.0	1.4	0.0
Yellow-headed Blackbird (Xanthocephalus xanthocephalus)	83.1	0.0	-97.2	-92.5	-72.4	-51.7
Eastern Meadowlark (Sturnella magna)	77.4	83.4	12.8	0.0	5.7	0.0
Orchard Oriole (Icterus spurius)	76.7	80.7	45.0	0.0	39.3	0.0
Baltimore Oriole (Icterus galbula)	81.9	89.0	-40.4	0.0	-18.0	0.0
Brewer's Blackbird (Euphagus cyanocephalus)	81.5	74.1	-100.0	-100.0	-95.9	-92.5
Evening Grosbeak (Coccothraustes vespertinus)	73.3	0.0	-100.0	-100.0	-88.5	-78.8
Purple Finch (Carpodacus purpureus)	86.8	6.2	-82.6	-69.2	-55.9	-53.5
House Finch (Carpodacus mexicanus)	72.9	5.5	-41.0	-54.3	-37.9	-37.8
American Goldfinch (Carduelis tristis)	86.9	95.3	-50.1	0.0	-21.9	0.0
Vesper Sparrow (Pooecetes gramineus)	86.5	83.7	-85.4	-70.0	-50.8	-23.7

Table 3.2 continued

Species	Total R^2	Rel. Climate variables	CCC		Hadley	
			Population	Range	Population	Range
Savannah Sparrow (Passerculus sandwichensis)	86.7	95.5	-94.0	-66.4	-80.5	-37.5
Grasshopper Sparrow (Ammodramus savannarum)	72.6	17.2	-23.5	-11.1	-4.7	-8.8
Lark Sparrow (Chondestes grammacus)	76.5	89.1	736.1	291.2	528.1	286.7
White-throated Sparrow (Zonotrichia albicollis)	89.2	0.0	-100.0	-100.0	-72.2	-72.4
Chipping Sparrow (Spizella passerina)	72.9	32.2	-51.6	0.0	-31.7	0.0
Clay-colored Sparrow (Spizella pallida)	85.3	94.7	-100.0	-100.0	-95.5	-94.1
Field Sparrow (Spizella pusilla)	73.3	18.0	23.7	0.0	10.6	0.0
Dark-eyed Junco (Junco hyemalis)	73.2	25.2	-93.7	-93.4	-70.2	-72.1
Bachman's Sparrow (Aimophila aestivalis)	66.3	27.1	83.1	134.3	25.3	57.6
Song Sparrow (Melospiza melodia)	87.9	89.9	-83.0	-61.8	-66.2	-30.2
Lincoln's Sparrow (Melospiza lincolnii)	55.7	0.0	-100.0	-100.0	-80.1	-68.2
Swamp Sparrow (Melospiza georgiana)	72.5	18.1	-94.8	-87.2	-64.0	-53.7
Eastern Towhee (Pipilo erythrophthalmus)	78.6	24.7	-30.2	0.0	-27.7	0.0
Northern Cardinal (Cardinalis cardinalis)	86.8	72.7	18.1	0.0	16.0	0.0
Rose-breasted Grosbeak (Pheucticus ludovicianus)	86.3	81.2	-79.3	-69.5	-46.4	-33.5
Blue Grosbeak (Guiraca caerulea)	82.4	88.0	88.6	66.3	69.6	66.3
Indigo Bunting (Passerina cyanea)	76.6	84.7	-7.9	0.0	2.4	0.0
Painted Bunting (Passerina ciris)	65.1	91.7	459.8	169.5	236.7	82.5
Dickcissel (Spiza americana)	81.7	32.1	78.5	75.0	54.0	44.9
Summer Tanager (Piranga rubra)	85.7	83.6	66.3	60.0	26.5	26.6
Purple Martin (Progne subis)	69.4	9.4	12.3	0.0	2.4	0.0
Cliff Swallow (Petrochelidon pyrrhonota)	69.1	95.9	-77.3	-70.7	-55.8	-43.8
Barn Swallow (Hirundo rustica)	77.4	73.8	-7.3	0.0	-0.9	0.0
Tree Swallow (Tachycineta bicolor)	85.5	15.0	-92.9	-76.3	-57.4	-45.2
Bank Swallow (Riparia riparia)	68.5	92.8	-85.9	-65.0	-66.1	-20.4
Cedar Waxwing (Bombycilla cedrorum)	83.0	87.9	-79.1	-62.1	-56.7	-30.0
Loggerhead Shrike (Lanius ludovicianus)	72.8	86.7	106.5	59.8	58.5	59.8
Red-eyed Vireo (Vireo olivaceus)	73.4	4.8	-10.0	0.0	-7.8	0.0
Warbling Vireo (Vireo gilvus)	76.4	10.0	-62.4	-11.1	-37.4	6.8
Blue-headed Vireo (Vireo solitarius)	78.9	1.4	-62.2	-45.5	-44.8	-32.6
White-eyed Vireo (Vireo griseus)	82.2	85.8	60.7	47.4	15.5	22.1
Bell's Vireo (Vireo bellii)	67.3	64.2	226.0	319.3	108.3	173.6
Black-and-white Warbler (Mniotilta varia)	66.4	13.9	39.5	28.3	40.4	31.0
Prothonotary Warbler (Protonotaria citrea)	76.7	8.3	-39.0	66.5	-34.0	32.4
Worm-eating Warbler (Helmitheros vermivorus)	51.7	7.5	4.2	26.0	29.8	26.1
Blue-winged Warbler (Vermivora pinus)	68.6	34.3	-75.4	-74.8	-71.9	-70.4
Golden-winged Warbler (Vermivora chrysoptera)	64.4	3.6	-82.0	-68.3	-73.3	-47.3
Nashville Warbler (Vermivora ruficapilla)	87.4	0.0	-100.0	-100.0	-71.4	-59.8
Northern Parula (Parula americana)	67.6	8.5	-4.6	31.2	-9.9	7.2

Table 3.2 continued

Species	Total R^2	Rel. Climate	CCC		Hadley	
		variables	Population	Range	Population	Range
Yellow Warbler (Dendroica petechia)	79.6	95.4	-76.2	-63.1	-50.3	-30.4
Black-throated Blue Warbler (Dendroica caerulescens)	79.0	6.3	-72.5	-80.9	-54.4	-64.6
Yellow-rumped Warbler (Dendroica coronata)	86.6	0.0	-100.0	-100.0	-72.2	-75.7
Magnolia Warbler (Dendroica magnolia)	81.1	18.9	-96.4	-93.2	-70.1	-65.6
Cerulean Warbler (Dendroica cerulea)	64.7	9.2	-46.2	-16.6	-20.5	7.1
Blackburnian Warbler (Dendroica fusca)	79.1	65.7	-100.0	-100.0	-88.4	-81.9
Yellow-throated Warbler (Dendroica dominica)	60.9	74.3	14.6	61.2	25.1	21.2
Black-throated Green Warbler (Dendroica virens)	77.4	0.0	-67.5	-45.4	-49.5	-25.8
Pine Warbler (Dendroica pinus)	80.1	0.0	-3.8	19.9	-25.3	-14.2
Prairie Warbler (Dendroica discolor)	65.6	11.3	9.5	23.9	17.1	32.7
Ovenbird (Seiurus aurocapillus)	79.9	17.4	-78.4	-63.3	-65.2	-49.4
Northern Waterthrush (Seiurus noveboracensis)	78.1	0.0	-98.3	-90.4	-69.8	-63.0
Kentucky Warbler (Oporornis formosus)	62.2	65.3	26.8	57.6	10.7	25.8
Mourning Warbler (Oporornis philadelphia)	78.4	20.8	-100.0	-100.0	-86.0	-81.1
Common Yellowthroat (Geothlypis trichas)	60.7	63.9	-69.8	0.0	-69.6	0.0
Yellow-breasted Chat (Icteria virens)	83.7	85.6	15.8	49.2	9.7	28.9
Hooded Warbler (Wilsonia citrina)	69.5	10.9	10.8	34.6	-7.1	-2.6
Canada Warbler (Wilsonia canadensis)	80.4	6.3	-78.9	-42.4	-56.8	-32.5
American Redstart (Setophaga ruticilla)	71.9	16.7	-32.8	10.6	-17.2	18.7
House Sparrow (Passer domesticus)	57.4	3.0	2.7	0.0	3.5	0.0
Northern Mockingbird (Mimus polyglottos)	86.9	96.2	46.7	0.0	22.0	0.0
Gray Catbird (Dumetella carolinensis)	77.4	78.0	-17.2	0.0	-13.5	0.0
Brown Thrasher (Toxostoma rufum)	62.5	50.5	-40.7	0.0	-21.7	0.0
Carolina Wren (Thryothorus ludovicianus)	90.2	93.6	58.2	52.4	18.3	24.7
House Wren (Troglodytes aedon)	87.2	93.8	-56.3	-53.8	-20.2	-24.6
Winter Wren (Troglodytes troglodytes)	80.9	11.6	-97.8	-90.3	-79.6	-62.6
Sedge Wren (Cistothorus platensis)	80.9	70.3	-92.5	-77.0	-68.8	-54.1
Brown Creeper (Certhia americana)	62.9	0.0	-83.5	-58.6	-63.3	-42.4
White-breasted Nuthatch (Sitta carolinensis)	68.1	24.6	14.7	12.2	17.4	5.1
Red-breasted Nuthatch (Sitta canadensis)	86.7	0.0	-100.0	-100.0	-74.7	-72.4
Brown-headed Nuthatch (Sitta pusilla)	87.0	77.2	41.5	89.4	-10.8	15.1
Tufted Titmouse (Baeolophus bicolor)	87.4	97.4	30.3	-3.0	18.0	0.4
Black-capped Chickadee (Poecile atricapillus)	84.2	79.5	-55.9	-34.8	-28.2	-24.7
Blue-gray Gnatcatcher (Polioptila caerulea)	69.5	81.8	53.3	0.0	28.5	0.0
Wood Thrush (Hylocichla mustelina)	81.5	9.0	-31.7	10.8	-29.5	1.8
Veery (Catharus fuscescens)	85.1	78.4	-81.6	-71.5	-56.8	-48.5
Swainson's Thrush (Catharus ustulatus)	64.2	0.0	-100.0	-100.0	-88.7	-67.1
Hermit Thrush (Catharus guttatus)	84.5	4.9	-82.0	-60.1	-53.6	-43.6
American Robin (Turdus migratorius)	91.0	95.4	-13.8	5.0	-3.4	4.6

For example, the rose-breasted grosbeak (Figure 3.6) population was projected to decrease by 79.3% under the CCC scenario and by 46.4% under the Hadley scenario. Similarly, the grosbeak's range was projected to decrease under the CCC and Hadley scenarios by 69.5% and 33.5%, respectively. In contrast, the white-eyed vireo (*Vireo griseus*) was projected to increase in its population and range by 60.7% and 47.4%, respectively, under the CCC scenario and by 15.5% and 22.1%, respectively, under the Hadley scenario. Despite the large variation among the species' projected responses to climate change, the two GCM scenarios showed considerable agreement across species in projecting the response of the species population ($r_s = 0.96$, $P<0.001$) and range ($r_s = 0.96$, $P<0.001$) (Figure 3.7).

The overall summary of the birds' projected response to climate change provided dramatic and clear results (Figure 3.8). Under the CCC scenario 61 species (41%) were projected to decrease by more than 50% in their eastern populations, while under the Hadley scenario 51 species (34%) were projected to decrease by more than 50 %. Of these species, 49 were projected by both scenarios to decrease by at least 50%. There were thus 12 species for which the CCC but not the Hadley scenario projected severe decrease, and only two species for which the Hadley but not the CCC model projected severe losses. These findings highlight the similarities in the predicted response of birds under the two scenarios: losses dominated the distribution of population change, though with a few species showing large increases (Figure 3.8). The distribution of changes in range size were also skewed towards losses (Figure 3.8), though 39 species showed no change in range under either scenario.

Figure 3.6. Maps of the rose-breasted grosbeak from A) the actual Breeding Bird Survey data; B) the current species incidence as predicted by the regression tree model; the predicted potential future incidence of the species after climate change according to the CCC (C) and Hadley (D) GCM; finally E) and F) show the differences between predicted current and predicted future species incidence according to the CCC and Hadley GCM scenarios, respectively.

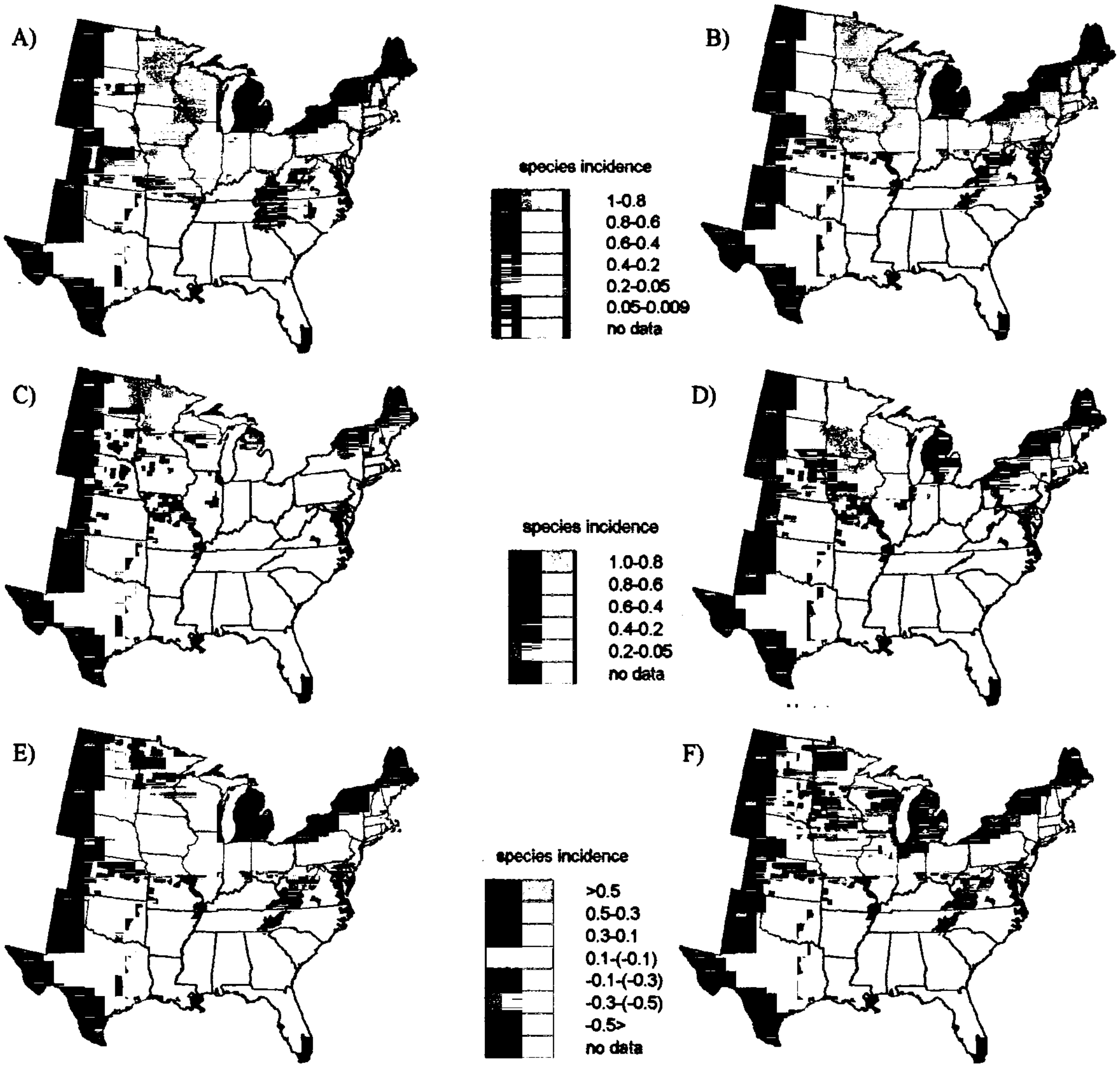
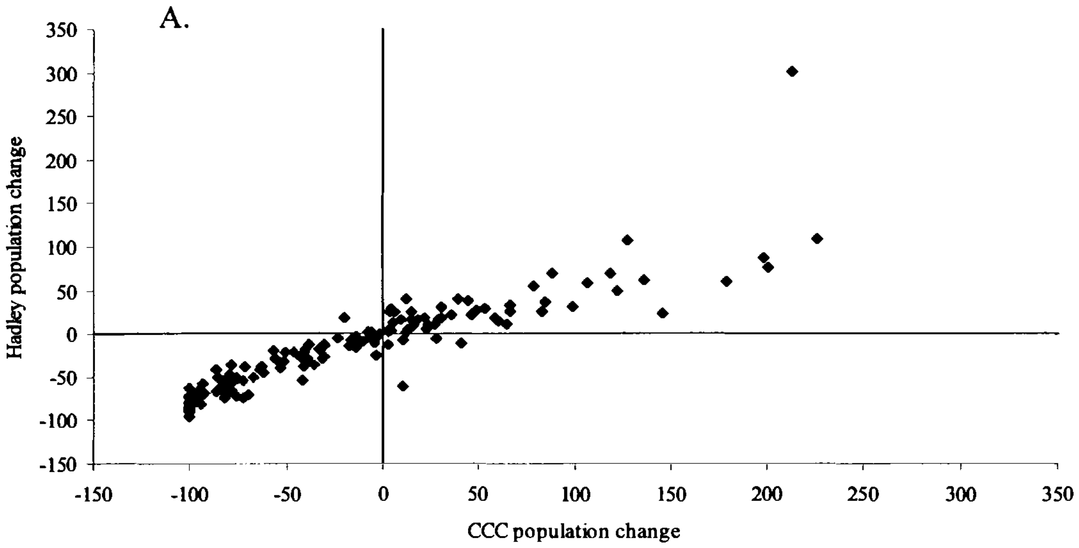


Figure 3.7. The projected changes in populations (A) and ranges (B) under the Hadley and CCC scenarios. Note that the Swainson's hawk and scissor-tailed flycatcher were not plotted because they were projected to increase by greater than 350% in population and range for both GCM scenarios. Similarly, the lark sparrow and painted bunting were not plotted on the population change figure as they were projected to increase greater than 350%. These species were omitted to show the pattern of the majority of the species.



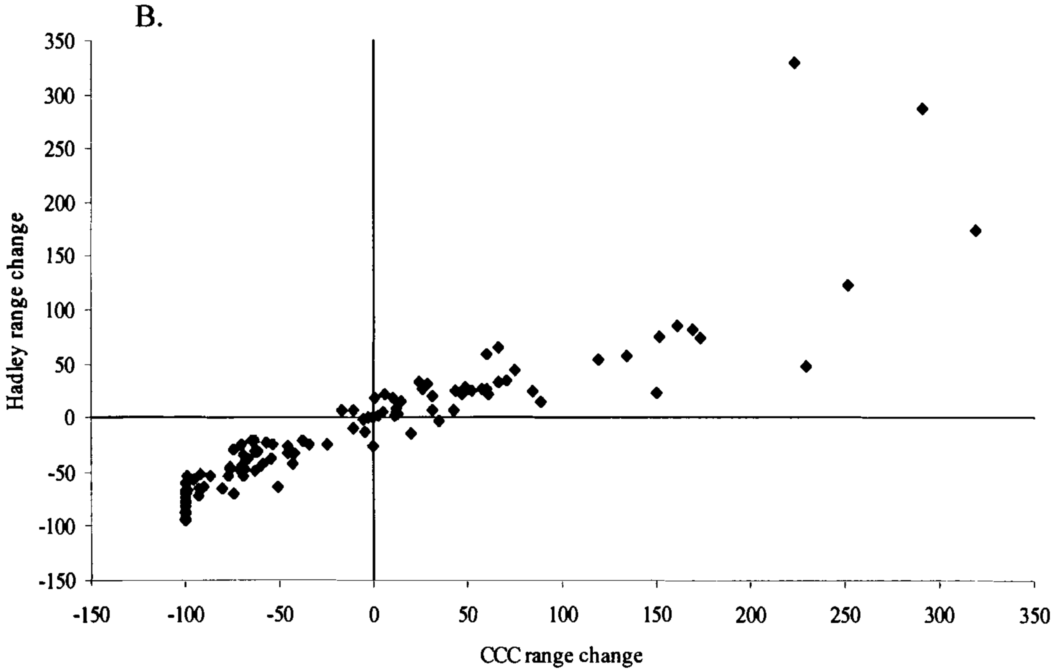
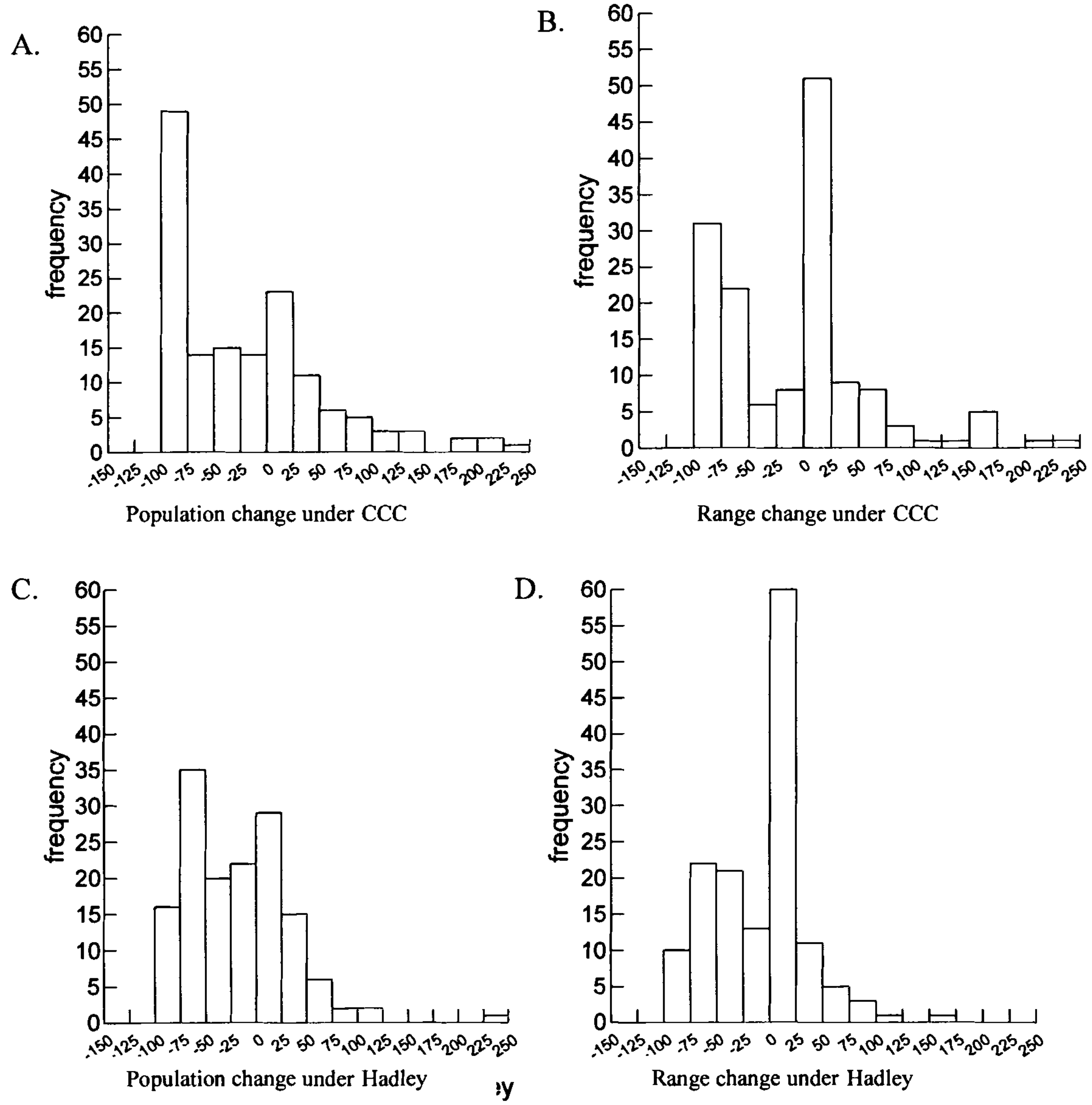


Figure 3.8. Frequency distribution of projected change in species populations (A and C), and range (B and D) under the CCC and the Hadley scenario respectively. Note there were outliers that were omitted below: the Swainson's hawk, scissor-tailed flycatcher, and lark sparrow were omitted in each plot, the Mississippi kite in C and D, the painted bunting in A, and the Bell's vireo in B.



Because the CCC and Hadley models differ in their predictions of temperature and precipitation, it was possible that the projections for individual species might be differentially sensitive to the type of predictor variable in their specis-specific model. To explorethis possibility, the potential impacts of climate change on groups of species that showed similar model characteristics, I arranged species into groups based on the relative contributions of variable types (i.e., climate, vegetation, or elevation) to their total model R^2. If a model received greater than 60 % of its total R^2 from climate, vegetation, or elevation variables, it was identified as a climate-, vegetation-, or elevation-dominated model, respectively (Figure 3.9). Species that did not receive greater than 60% of their total R^2 from these groups were not attributed to any of these classes (fifteen models fell into this category). The vegetation-dominated models contained a high proportion of the species with populations projected to decrease by at least 25% (under the CCC and Hadley scenarios, chi-square=14.54 and 13.26 respectively[1]), while the climate-dominated models contained a high proportion of species projected to increase in population (under the CCC and Hadley scenario, chi-square=13.14 and 7.14 respectively[1]) (Table 3.3). Changes in range followed this same general pattern, but were less dramatic. The changes in range for the Hadley vegetation-dominated model and CCC climate-dominated models showed significant differences from the overall results (chi-square=12.27, and 9.70 respectively), while the others were not significantly different from the overall results (Table 3.3).

Finally, I examined consequences of projected climate change on birds breeding in specific habitats. I classified the species into breeding guilds of grasslands,

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[1] These analyses were compared with expected values generated from the proportions of the overall results and determined significantly different at $X^2_{0.05,2}=5.99$.

Figure 3.9 Frequency distribution of the relative contribution of climate and vegetation variables in the 152 species models.

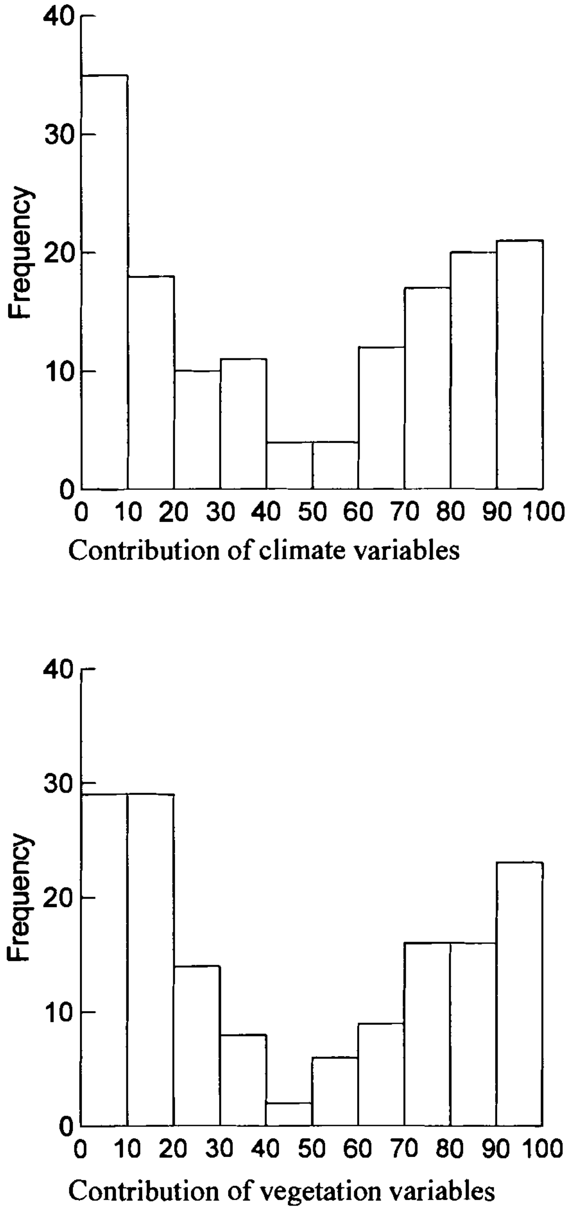

Table 3.3. The proportion of the species projected to increase, decrease, and show little change in their eastern United States populations and range (changes where identified at greater than 25% from the species current population). The relative proportion of the species' model that was made up by climate, vegetation, and elevation variables classified the species. If a model received greater than 60 % of its total R^2 from climate, vegetation, or elevation variables, it was identified as a climate-, vegetation-, or elevation-dominated model, respectively. If there was an equal contribution of climate and landscape variables in the model, they were classified as none dominant.

Species model Characteristics		Pop. decrease (< -25%)	Little change (-25 to 25%)	Pop. increase (>+25%)
Vegetation-dominated (n = 65)	CCC	69.2	26.2	4.6
	Hadley	67.7	26.2	6.2
Climate-dominated (n = 70)	CCC	37.7	20.0	42.9
	Hadley	31.4	40.0	28.6
Elevation-dominated (n = 3)	CCC	66.7	0.0	33.3
	Hadley	66.7	0.0	33.3
None dominant (n = 14)	CCC	35.7	42.9	21.4
	Hadley	21.4	42.9	35.7

		Range decrease (< -25%)	Little Change (-25 to 25%)	Range increase (>+25%)
vegetation-dominated (n = 65)	CCC	53.8	35.4	10.8
	Hadley	55.4	35.4	9.2
Climate-dominated (n = 70)	CCC	31.4	35.7	32.9
	Hadley	22.9	55.7	21.4
Elevation-dominated (n = 3)	CCC	0.0	33.3	66.7
	Hadley	0.0	33.3	66.7
None dominant (n = 14)	CCC	14.3	71.4	14.3
	Hadley	7.1	78.6	14.3

woodlands, wetland, scrub/scrub, and urban habitats, following Sauer et al. (2001). Grouping species into guilds has been widely used to understand similarities and differential patterns among guilds (e.g. Holmes and Recher 1986, Root 1988a). The percentages of species in the five guilds projected to increase and decrease in their eastern populations were consistent across all guilds and with the summary of all species. For each guild, the respective percentage of species projected to decrease by 25%, show little change, and increase by 25% are: grassland - 70%, 20%, and 10%; woodland - 55%, 23%, and 22%; wetland - 62%, 9%, and 29%; urban - 36%, 55%, and 9%; and scrub/shrub - 54%, 23%, and 23%. The limited sample sizes for the grassland (8 species) and urban (11 species) guilds restricted the ability to evaluate their differences from the overall summary results.

3.5 Discussion

The potential impact of global climate change on organisms has stimulated considerable research (e.g., Hansen et al. 2001, Kareiva et al. 1993, Schneider and Root 2002). In fact, adjustments in species movements and habits are now being linked to changes in current climate conditions (Parmesan et al. 1999, Tomas and Lennon 1999, Both and Visser 2001, Walther et al. 2002). Several authors predicted significant changes in bird species ranges and abundances as a consequence of climate change in North America (Price and Root 2001, Sorenson et al. 1998) and South Africa (Erasmus et al. 2002). These studies used only climate variables to predict the response of species to climate change. My results which include both climate and vegetation variables in model construction predict major shifts in many bird species ranges and population in the eastern Unites States under the CCC and Hadley GCM scenarios. Under the CCC and the Hadley scenarios, respectively the eastern U.S. populations of 51.3% and 46.7% of the 152species investigatedwere projected to decrease by 25% or more, and the populations of 24.3%and 19.7% of the species were projected to increase by 25% or more. Similarly, I predicted substantial changes in the bird species' ranges in the eastern United States under the two GCM scenarios. Projected losses to the species range of greater than 25% occurred in 38.8% and 34.9% of the species under the CCC and Hadley scenarios, respectively, while gains in species ranges occurred in 22.4% and 19.7% of the species, respectively. Many species thus showed only small changes in their range, even though their abundance was projected to change substantially. That is, such species are likely to continue to occupy large portions of their current ranges while undergoing substantial changes in their abundance within their range.

A crucial component of this analysis is that it is the first to include both climate variables and tree species distributions as potential predictors of the individual bird species patterns. Root and Schneider (2002) pointed to the need for an understanding of how the vegetation patterns of a future landscape altered by climate change will influence species distributions. For many bird species there may be a direct relationship to tree species abundance, as with the nuthatch species that forage on trees. However, for other species, the occurrence of tree species variables in the bird models may be a surrogate for other environmental information. For example, paper birch (*Betula papyrifera*) was dominant in the common loon model, and balsam fir (*Abies balsamea*) was also present. There is no direct mechanistic link between the common loon and these tree species, but the trees' presence is associated with various soil characteristics and other environmental factors (Iverson and Prasad 1999). These environmental conditions may indicate a particular habitat (or climate) that the common loon occupies. Therefore, the presence of specific tree species might act as a surrogate to describe landscape features important in modeling bird abundance patterns that cannot be described solely by climate variables. In support of this possibility, only seven of 152 of my predictive models lacked vegetation variables and only one model contained only climate variables. This result underscores the importance of including landscape features in predicting bird species distributions, even at relatively large extents.

One of the most striking findings here was the differential between models dominated by vegetation variables and models dominated by climate variables. A high proportion of species models that were dominated by vegetation variables projected population declines following climate change. In contrast, most species models that were dominated by climate variables projected an increase in population levels relative to the overall results. An explanation for this phenomenon could be that species with climate-dominated models showed little association with landscape features provided in this analysis. Therefore, they were not constrained by underlying vegetation features during projection and were predicted to inhabit areas as long as the climate was suitable. In contrast, the vegetation-dominated species models led to distributions and abundances constrained by a future climate envelope that included both suitable temperatures and the appropriate vegetation structure. This double constraint on the bird species range resulted in a smaller area of potential suitable habitat for the species to occupy following climate change. This smaller area of suitable habitat may be further constrained by the time lags required for the tree species to redistribute (Pacala and Hurtt 1993).

While the two GCM scenarios produced substantively different predictions for individual species' responses to climate change, the predictions usually differed only in the magnitude and not the direction of the anticipated change. As a result, the two GCM scenarios used in this analysis produced similar overall results as demonstrated by the strong positive relationships between the CCC and Hadley based predictions for changes in abundance and range. These overall similarities in predictions are rather surprising considering the large differences in temperature change between the two scenarios: the CCC scenario predicted a more dramatic increase in average temperature (5.64 °C) from the current temperature (based on long term averages from1969-1990) whereas the Hadley scenario of global climate change predicted milder increases in temperature (2.66 °C). This indicates that significant changes in avian species compositions could occur if the projected changes in the eastern United States' climate patterns are within the bounds of these two different GCM scenarios.

This analysis of 152 bird species allowed for a comprehensive look at the potential response of birds to projected climate change in the eastern United States. However, not all species that occur in the eastern United States could be modeled. The Breeding Bird Survey is a valuable data set that allows for research at large extents in space and time, but the protocol of the BBS does not work well for all species (Robbins et al. 1986). Some species are underrepresented in the point counts, which prevent them from being modeled effectively. Another source of poor model confidence in some species could arise from a deficit in appropriate predictor variables.

The restriction of the study area to the eastern United States might have introduced some biases in the study. First, many of the species modeled here winter in the tropics and changes on their wintering grounds were not possible to address here. The predicted changes in the species' abundances and ranges are only applicable to the extent of this study. This is an important point, because all 152 species in this analysis had a current or projected range that came in contact with the boundaries of the study area. Therefore, it is likely that species with considerable projected losses will move outside the study area. With increasing temperatures they would likely move north into Canada or west into the Rocky Mountains. Likewise, it is possible that species, which showed large increases in their range and abundance within the study area suffered losses outside the study area. Despite these shortcomings, this analysis provides considerable information on the potential changes of bird populations within the extent of this study.

As with all attempts to predict the response of species to projected global climate change, one has to consider several assumptions. GCMs are a tremendous asset and their ability to predict current and past climate patterns suggests their potential to represent future climate conditions (IPCC 2001). However, there is no way to validate their outputs, as they are projections of future climate conditions. Therefore, using more then one scenario is recommended because this provides for a range of possible outcomes and thus the sensitivity of models to variations in projections can be observed (Hansen et al. 2001). In addition, various assumptions underlie the modeling of bird species' responses to climate change. The species models created under current conditions related abundance patterns to climate, tree species distribution, and elevation. Using these relationships for predicting future distributions under climate and vegetation change assumes that these relationships will remain constant under such changes. In light of these assumptions, the results of any attempt to project future distribution of species should not be taken as exact forecasts (Iverson and Prasad 1998), but as an evaluation of the potential consequences of rapid climate change on species distributions.

Chapter 4

QUANTIFYING THE IMPACTS ON BIODIVERSITY OF POLICIES FOR CARBON SEQUESTRATION IN FORESTS

4.1 Abstract

There is currently a great deal of interest in the use of afforestation (conversion of non-forest land to forest) to reduce atmospheric concentrations of carbon dioxide. To date, economic analyses have focused on the costs of forest carbon sequestration policies related to foregone profits from agricultural production. No studies have examined additional costs or benefits associated with impacts on biodiversity. The main objective of this paper is to estimate the changes in farmland and forest bird populations that are likely to occur under an afforestation policy. Econometric models of land use are used to simulate the response of private landowners to subsidies for tree planting on agricultural land. We evaluate subsidies that achieve conversion of 10 percent of the total agricultural land in each of three U.S. states (South Carolina, Maine, and southern Wisconsin). Bird density estimates are derived for 615 species with data from the national Breeding Bird Survey. Percentage changes in agricultural and forest land for each county are applied to county-level estimates of bird densities for farmland and forest birds.

Despite considerable spatial variation in agricultural land conversion rates and farmland bird distributions within these states, statewide losses of farmland birds were relatively uniform at 10.8–12.2 percent. Increases in forest bird populations, however, varied substantially between states: 0.3 percent in Maine, 2.5 percent in South Carolina, and 21.8 percent in southern Wisconsin. Surprisingly, a net loss in total bird populations

results in all three states (–2.0 percent in Maine, –2.3 percent in South Carolina, and –1.1 percent in southern Wisconsin), despite the prevailing wisdom as to bird-rich forests. The loss is due to the coincidence of centers of high farmland bird richness and low forest bird richness with areas economically suited to conversion. Additional gains in forest species may result, however, if afforestation within the economically optimal counties is concentrated to fill in existing forest fragments presently suffering avian losses to edge predators. Our results thus show that assessments of the biological consequences of afforestation for carbon sequestration must consider both current land cover and the distributional patterns of organisms as well as the policy's conversion goal.

4.2 Introduction

The Kyoto Protocol to the Framework Convention on Climate Change, adopted by a majority of the world's nations in December, 1997, sets specific targets and timetables for the reduction of greenhouse gas emissions by Annex I (industrialized) countries. There is currently a great deal of interest in converting non-forest to forest land (afforestation) to offset carbon dioxide (CO_2) emissions. Trees and other forest vegetation photosynthesize CO_2 to yield carbon and since forests generally store more carbon than land in other uses (e.g., agriculture), afforestation can achieve a reduction in net greenhouse gas emissions. Article 3.3 of the Protocol states that carbon sequestered as the result of human-induced afforestation, reforestation, and deforestation is to be included in the emissions inventory used to determine a nation's compliance with its treaty obligations.

The decision to pursue an afforestation strategy depends, in part, on the costs of afforestation relative to costs of alternative approaches such as improving energy efficiency, switching to cleaner fuels, as well as other methods of carbon sequestration (National Academy of Science 1992, Holdren and Lee 1999). A number of authors have estimated the marginal costs of sequestering carbon in forests.[1] For example, Plantinga et al. (1999) estimate econometric models of land use in which the shares of land allocated to forestry and agriculture are functions of net returns to alternative uses and other decision variables. The fitted models are then used in a simulation of a subsidy program for afforestation. The subsidies increase the relative net returns to forestry, which increases the area of land allocated to forest and the amount of carbon sequestered. Marginal cost schedules are constructed by arraying subsidies per unit of carbon against total carbon sequestered.

In general, previous studies find that the costs of carbon sequestration in forests are comparable to, and in some cases lower than, costs of alternative mitigation and abatement approaches. However, these analyses are focused solely on the opportunity costs of agricultural production. An important issue not considered in these studies is the impact of the resulting land use changes on biodiversity.[2] Although agricultural land is generally regarded as purely an anthropogenic habitat, it is in fact a significant resource for a variety of species of conservation interest (e.g., for grassland birds) (Herkert 1994, Vickery et al. 1994). Similarly, any advantages in the form of enhanced populations of

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[1] Among the studies providing marginal cost estimates are Moulton and Richards (1990), Adams et al. (1993), Richards et al. (1993), Parks and Hardie (1995), Adams et al. (1997), Alig et al. (1999), Plantinga et al. (1999), Stavins (1999), Newell and Stavins (2000), and Plantinga and Mauldin (2001).

[2] Afforestation of agricultural land may have other environmental impacts. For example, in regions where intensive agriculture is practiced, afforestation typically reduces soil erosion and the contamination of ground and surface water by agricultural chemicals.

forest species that might result from afforestation are of relevance to conservation efforts, particularly in the case of neotropical migrant birds, many species of which are markedly declining in numbers (Robbins et al. 1989b, Robinson et al. 1995).

Thus, a more comprehensive analysis of carbon sequestration costs would consider not only foregone profits from agriculture, but the additional environmental benefits and costs associated with afforestation. In the present paper, we estimate the changes in bird populations likely to arise under the carbon sequestration policy modeled in Plantinga et al. (1999). Our specific objective is to determine the percentage changes in farmland and forest birds resulting from a policy that achieves conversion of 10% of the total agricultural land in each of three U.S. states (South Carolina, Maine, and southern Wisconsin). We use birds as a template for other biodiversity calculations in this context because the taxon is so data-rich, but the methods developed here can be extended to other taxa, although with less reliable data. Given current momentum toward the use of carbon management strategies to address global climate change, we assume that carbon sequestration is the primary policy objective. However, our study develops the tools needed for analysis of policies with multiple objectives. This is a first step towards the ultimate development of a national carbon sequestration strategy designed to mitigate climate change as well as to achieve other national environmental goals.

4.3 Methods

4.3.1 Land-use change in response to subsidies for carbon sequestration

In an earlier study, Plantinga et al. (1999) simulate the response of private landowners to subsidies for carbon sequestration in forests. In the present study, we analyze the biodiversity impacts of the land-use changes associated with the afforestation policies. We provide a summary of the methods used in the Plantinga et al. (1999) study and present the results relevant to the current analysis. Readers are referred to the original study for more details.

Plantinga et al. (1999) simulate carbon sequestration programs in Maine, South Carolina, and Wisconsin. These states were selected because they represent a broad range of current land-use patterns, physiographic conditions, and apparent opportunities for afforestation. Maine is a heavily forested state with little additional land available for conversion to forest. In contrast, South Carolina and Wisconsin have large amounts of agricultural land that potentially can be afforested. Maine and Wisconsin are northern states with short growing seasons relative to South Carolina. Southern pine tree species, valuable for lumber and plywood production, are abundant in South Carolina. Maine and Wisconsin have a mix of hardwood species (e.g., oak, maple, birch) and softwood species (e.g., spruce, fir) used in paper production.

Econometric land-use models were estimated using standard methods developed in Lichtenberg (1989), Wu and Segerson (1995), and Hardie and Parks (1997). The county shares of land in private forest (s_{it}^f), agricultural uses (s_{it}^a), and urban and other uses (s_{it}^u) are specified as logistic functions of exogenous variables (X_{it}):

$$(1) \qquad s_{it}^f = \frac{e^{\beta_f' X_{it}}}{1+e^{\beta_f' X_{it}}+e^{\beta_a' X_{it}}}, \qquad s_{it}^a = \frac{e^{\beta_a' X_{it}}}{1+e^{\beta_f' X_{it}}+e^{\beta_a' X_{it}}}, \qquad s_{it}^u = \frac{1}{1+e^{\beta_f' X_{it}}+e^{\beta_a' X_{it}}},$$

where i indexes counties, t indexes time, and β_f and β_a are vectors of parameters to be estimated. The three land-use shares account for all land in the county, implying $s_{it}^f + s_{it}^a + s_{it}^u = 1$ and that one of the shares is redundant. The additivity constraint is incorporated into (1) by expressing s_{it}^u in terms of the remaining shares (i.e.,

$s_{it}^{u} = 1 - s_{it}^{f} - s_{it}^{a}$). The exogenous variables include the county average per-acre net return to forestry; the county average per-acre net return to agriculture; county population density, which controls for the diversion of land to urban and other uses; composite land quality measures, including the average quality of land in the county and the proportion of the county's land in the highest land quality classes; and a constant term and time dummies.

Separate models were estimated for each state using pooled time-series and cross-sectional data. Data were collected for all 16 counties in Maine for the years 1971, 1982, and 1995, all 46 counties in South Carolina for the years 1986 and 1993, and 49 counties in the southern two-thirds of Wisconsin for the years 1983 and 1996. Only the southern counties of Wisconsin were included because much of the land in northern Wisconsin is publicly-owned and already forested. See Plantinga et al. (1999) for details on the econometric procedures used to estimate (1) and the estimation results.

The land-use models were then used in a simulation of carbon sequestration programs. The basic approach was to simulate per-acre subsidies to forestry by augmenting the corresponding net return measure in the econometric model. This implied increases in forest area and declines in agricultural area relative to land use in the baseline. Simulations were conducted for different levels of a per-acre subsidy and the corresponding land-use changes were converted to carbon units using yield functions developed by Birdsey (1992). A marginal cost schedule was constructed by arraying the subsidies—expressed in dollars per unit of carbon—against total carbon sequestered. The highest marginal costs were estimated for Maine, followed by South Carolina and, lastly, Wisconsin. The low costs in Wisconsin were due to the relative abundance of marginal lands with low opportunity costs for agricultural production. Opportunity costs were sufficiently low in Wisconsin to more than offset the somewhat higher carbon sequestration rates in South Carolina.

In the current study, we focus on land-use changes under scenario 1 in Plantinga et al. (1999). This scenario runs for 60 years beginning in 2000. In the baseline, all of the exogenous variables in the econometric model (net returns, population, etc.) are held constant at mid-1990s values and no timber harvesting is permitted on land enrolled in the program. Only agricultural lands are eligible and land must remain in the program for 10 years. In exchange, participating landowners receive a per-acre payment plus the costs of tree establishment. Since all the exogenous variables are constant in the baseline and subsidy levels remain constant over time, land enrolled in the first year of the program remains enrolled for the duration of the program. In scenario 1, the subsidy is uniformly applied across counties. Accordingly, marginal enrollment costs are equated across counties and the total cost of achieving a given amount of land conversion is minimized.[3]

4.3.2 Bird data

Maine, South Carolina, and Wisconsin provide diverse settings in which to study impacts on birds. Bird populations differ substantially between the three states, with South Carolina having a large component of year-round resident species while the avifauna of Wisconsin and Maine have a much higher proportion of migrant species.

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[3] One could argue that this does not represent the true least-cost solution since the program targets acres rather than carbon (see Parks and Hardie, 1995). However, within each state, there is little variation in carbon sequestration rates across counties, and the gains in efficiency from targeting carbon would likely be outweighed by the additional costs of administering such a program.

Bird populations in the three states differ markedly as to the environmental and land cover variables associated with their prevailing levels of species richness (O'Connor et al. 1996), providing an ecological diversity paralleling the economic diversity described above.

The bird data for the three states were derived from the national Breeding Bird Survey (BBS), a bird population monitoring program conducted annually since 1966 in the United States and Canada, currently by the Biological Resources Division of the U.S. Geological Survey and by the Canadian Wildlife Service. The scheme is administered by USGS staff at the Patuxent Wildlife Research Center in Laurel, Maryland, and currently acquires bird data from some 4,000 routes across the continent, though not all routes are surveyed annually (Robbins et al. 1989a). The survey focuses on diurnal birds that can be counted along a pre-determined route on secondary roads (three minute counts of all birds detected at 50 stops along a 25 mile route). Crepuscular and nocturnal species, and species restricted to off-road habitats, are, therefore, not surveyed. The survey was designed to obtain representative results across North America, within the constraints of this survey protocol, and a recent peer review concluded that the scheme results in data that, with only minor biases, largely meet its goals (O'Connor et al. 2000). O'Connor et al. (1996) extracted a set of 1200 representative BBS routes that had frequent and high quality surveys over the period 1981-90, and determined for each route the incidence of each species (the proportion of surveys along the route that had recorded the species). Yang et al. (1995) interpolated these incidence data for each of the 615 individual species to obtain an abundance surface over the conterminous U.S. for each individual species.

The grid used was the hexagonal grid of White et al. (1992), with some 12,600 points over the conterminous U.S.

For the present project we have estimates of land use changes for each county. We therefore overlaid the hexagonal grid on a county boundary layer and determined the polygons generated by intersections of county and hexagon borders. Each polygon received the incidence value of its source hexagon for that species and a county-wide incidence estimate was obtained by area-weighting the incidence values for the polygons. To determine how many birds would be lost from agricultural land or gained by new forests we consulted the species lists of Lauber (1991), Peterjohn and Sauer (1993), and Rodenhouse et al. (1995) to determine which species should be assigned to each of these habitats.[4] Species not in either list were omitted, examples being shorebirds and wetland species. We then assembled the incidence data for all of the forest species and added the incidence values for each county to get an index of abundance of forest birds since incidence measures are normally proportional to absolute abundance (Hanski 1992). We repeated this for the species in the list of farmland species. Note that the resulting abundance measures for forest and farmland birds assign equal weights to each species and, thus, assume that all species have the same conservation value. Below, we discuss alternative approaches that recognize differences in conservation importance.

In our calculations below we assume that bird densities remain constant, which is equivalent to assuming linear relationships between relative changes in bird populations and percentage changes in land use area. With rare exceptions (e.g., the house sparrow

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[4] Interested readers may contact the authors for a list of scientific names and habitat classifications for the 159 species used in this analysis.

Passer domesticus) agricultural species do not display strong curvilinear relationships with local habitat abundance (O'Connor et al. 1999). For many widespread forest species, on the other hand, incidence falls off rapidly as forest stands break up (Askins 1993) and we therefore explicitly consider below the possible effects of this on our results.

To compute statewide estimates of bird population changes, we weighted each county's results to account for the differential distribution of farmland and forest and its birds across the state. Proportional changes in the habitat were multiplied by the bird density in the habitat and then by the area of habitat to arrive at a county change in bird population. To compute the proportional change in birds at the state level, we summed the county changes in bird populations and divided by the sum of the total populations of the counties calculated in an analogous fashion.

4.4 Results

4.4.1 Land-use changes

Figure 4.1 shows for each state the mid-1990s distribution of agricultural land and the distribution of land that would convert to forestry under the state-wide scenario of conversion of 10 percent of agricultural land for carbon sequestration.[5] Current land use and changes in land use are reported in percentage terms to control for differences in county land areas.[6] In Wisconsin agriculture is prominent in the southeastern parts of the

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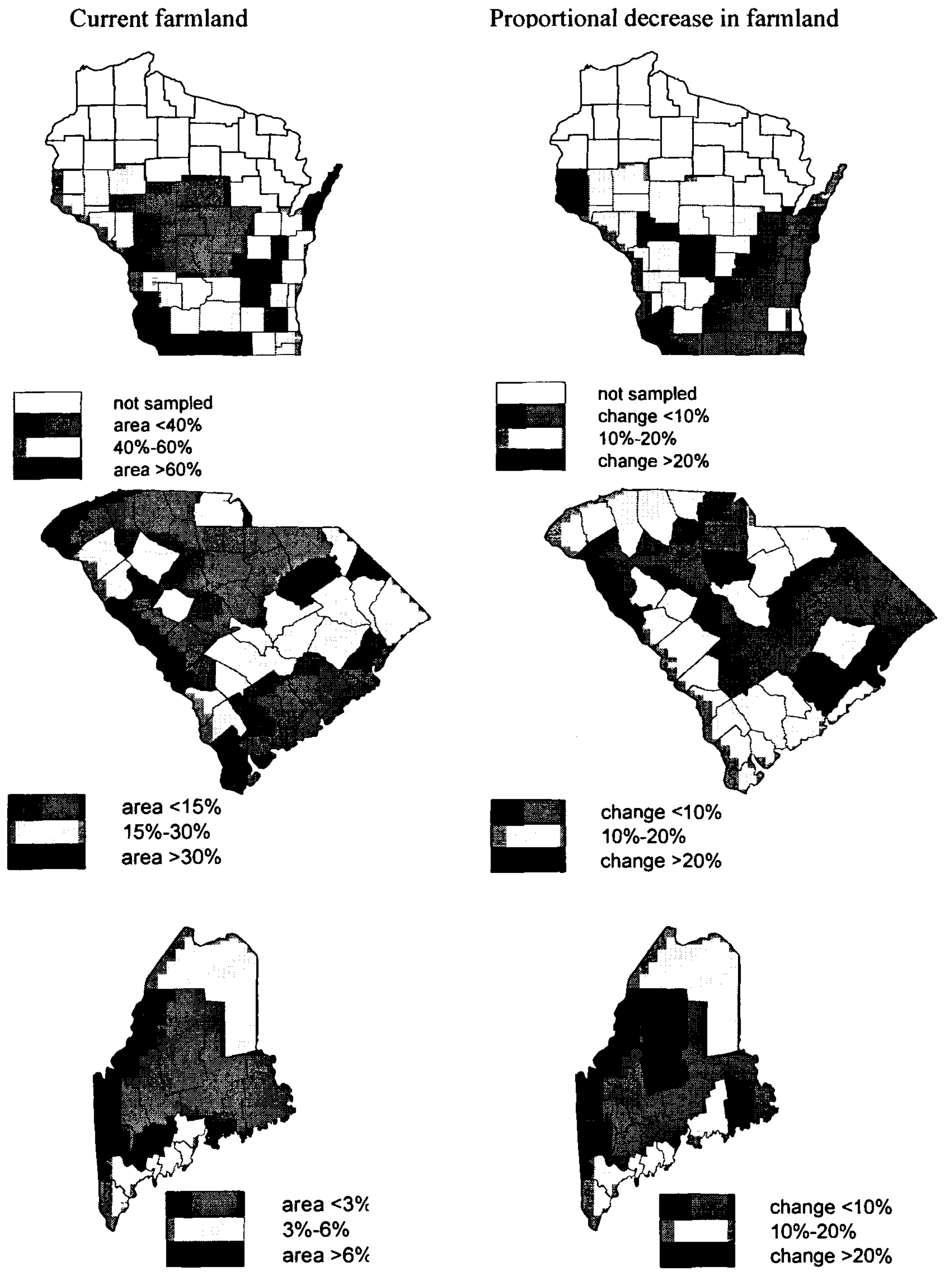
[5] Plantinga et al. (1999) consider conversion rates ranging from zero to 25 percent of state-wide agricultural land. The distribution of the estimated land-use changes across counties does not vary significantly with the state-level rate of agricultural land conversion.

[6] For the same reason, we emphasize percentage changes in bird populations. This makes our results easier to compare across counties and states, though at the expense of obscuring information on absolute change.

Figure 4.1. Current distribution of agricultural land (left) and simulated change in agricultural land under a carbon sequestration policy (right) in southern Wisconsin, South Carolina, and Maine.



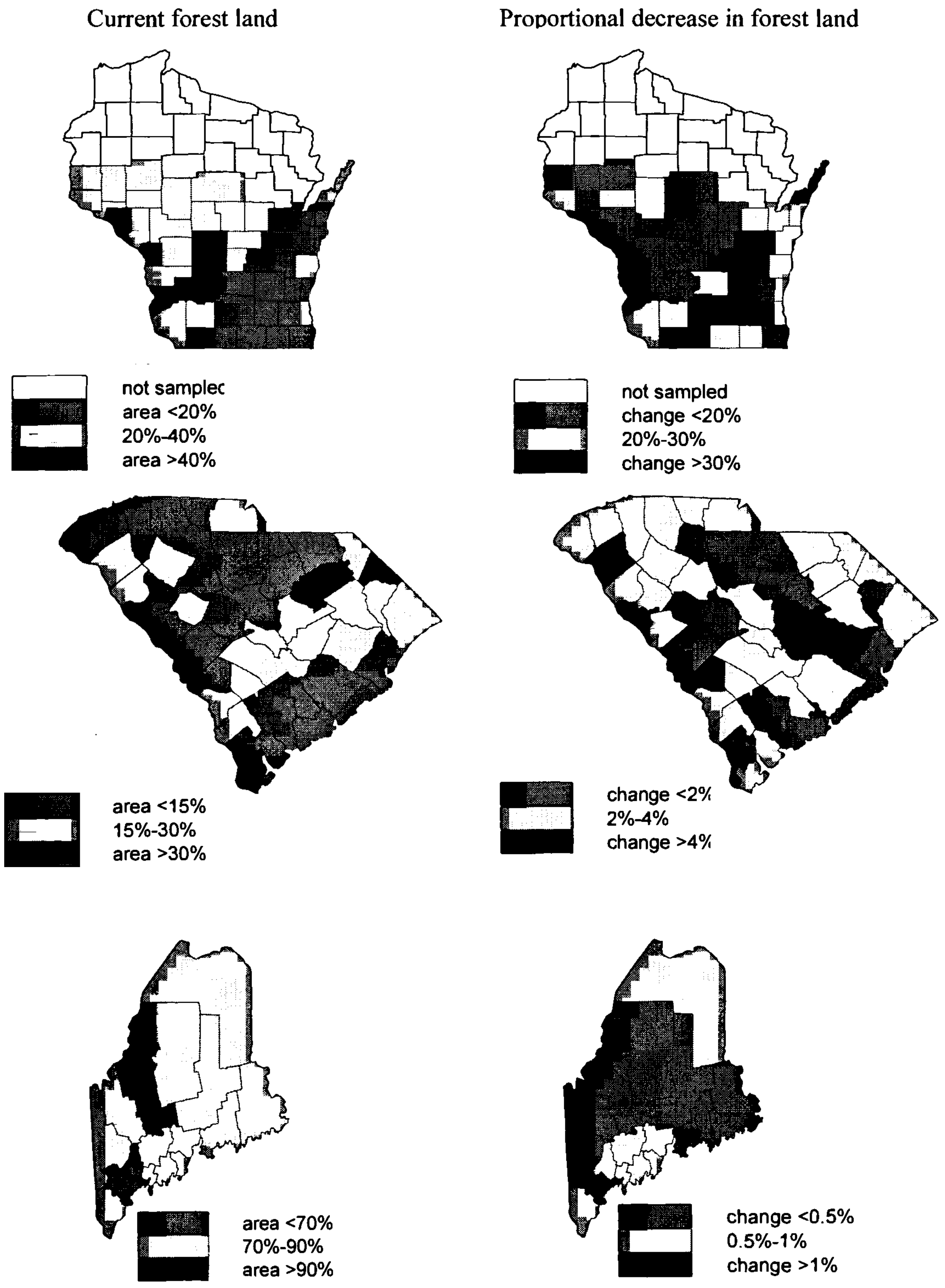
Current farmland

Proportional decrease in farmland

state, particularly along a belt of counties between Green Bay and Madison and in a southern belt of counties bordering Illinois. However, the decrease in agricultural land under the carbon sequestration policy is concentrated into the counties with less intensive and profitable agriculture, being greatest in Jackson, Juneau, and Adams counties and in a group of counties surrounding them in west central Wisconsin. Similarly, in South Carolina, agriculture is concentrated in a broad band of counties across the Atlantic Flatlands, with a scattering of more productive counties such as Anderson and Abbeville to the northwest and York in the north. However, the counties that would experience the greatest relative loss of agricultural land—Georgetown and Berkeley on the Coastal Plain and Fairfield and McCormack inland—are outside these areas, and most (though not all) of the counties that would experience conversion rates of 10-20 percent currently have less than 15 percent of their land in agriculture. Finally, in Maine agriculture is largely concentrated in the southern coastal counties, except for the potato lands of Aroostook county in the north, but with so little agriculture in Maine most of these counties would also experience conversion of land in pursuing the carbon sequestration policy. Land values in the two most intensively agricultural counties—Androscoggin and Kennebec—are such that conversion there would be low but all the other moderately farmed counties except Waldo in the east would join inland Piscataquis and coastal Hancock counties in disproportionate conversion.

Conversion of a given area of land to forestry can have a small or a large relative effect on the extent of forests in a county, depending on the existing forest base. This is shown in Figure 4.2 which maps both current forest lands and the relative increases brought about by the 10 percent conversion policy. The distribution of forests in

Figure 4.2. Current distribution of forests (left) and simulated change in forest area under a carbon sequestration policy (right) in southern Wisconsin, South Carolina, and Maine.

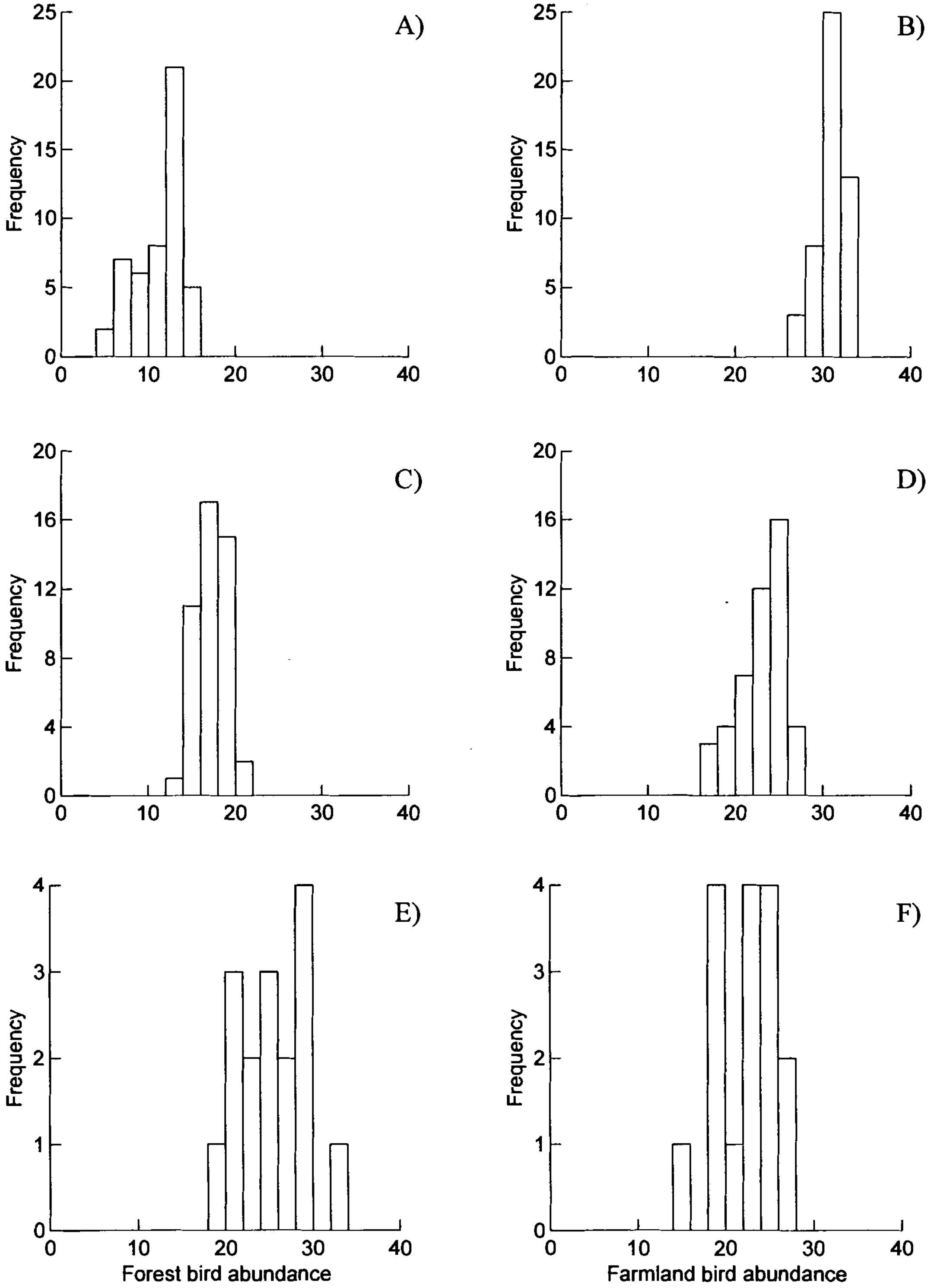


Wisconsin is largely complementary to that of agricultural land and concentrated in the northwest of the area modeled here. As a result, the greatest relative increases in forest are not where the relative loss of agricultural land would be greatest (Figure 4.1) but along its southeastern fringe: the largest relative increases in forest lands occur in a belt of counties extending northeastward and southwestward from Madison. In South Carolina, on the other hand, very few counties have less than 50 percent of their land already in forest and the relative increases in forest would be only a few percent (i.e., an order of magnitude smaller than in Wisconsin), and patchy in distribution. Similarly, with so much of Maine heavily forested the extra land in forest would result in increases of only one percent or less for most counties (Figure 4.2).

4.4.2 Bird distribution changes

The densities of birds within a county differed markedly between states, between habitats, and among counties (Figure 4.3). Median densities in Wisconsin were low in forests (median 12.2, range 5.7-15.9) but much higher on agricultural land (median 31.5, range 27.5-33.3) but in South Carolina were closer together (forest median density 16.9, range 13.9-21.7; agricultural land density 23.8, range 16.5-26.5). In Maine there was considerable overlap in densities in the two habitats (forest median 25.5, range 19.6-32.2; agricultural land median 23.4, range 14.4-26.3). Examination of Figure 4.3 shows that forest densities were about equally variable in all three states, though with different median densities, but agricultural bird densities became more variable from Wisconsin to Maine, probably reflecting the increase in the variability of agricultural conditions in the less agricultural states.

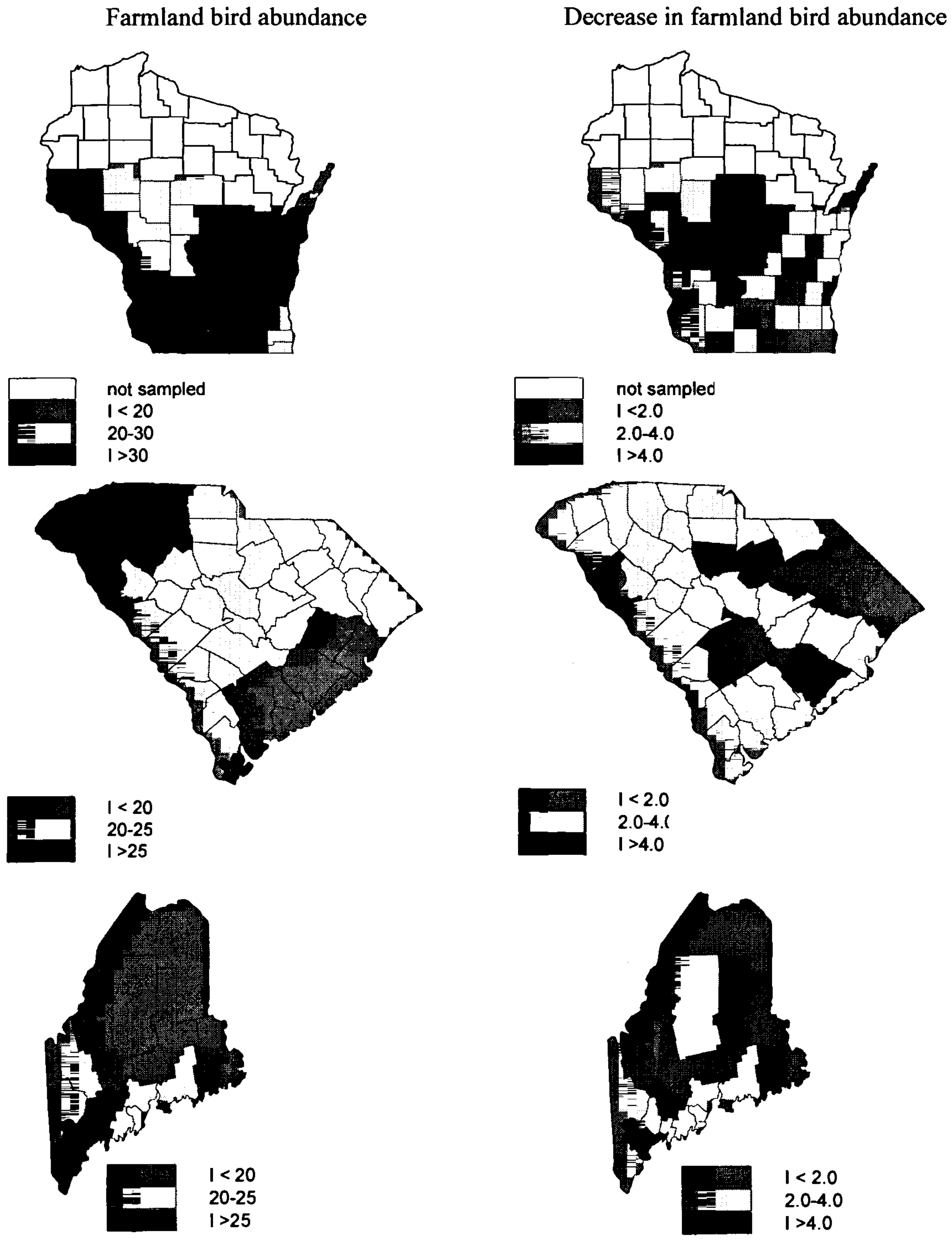
Figure 4.3. Frequency distributions of forest birds (left) and farmland birds (right) across counties in southern Wisconsin (A, B), South Carolina (C, D), and Maine (E, F).



Since bird densities are not uniform across each state, the consequences of land conversion for bird populations depend on the product of land use changes and local bird densities. Although locally the relative change in farmland bird numbers must exactly mirror the relative changes in agricultural land shown in Figure 4.1, a 10 percent (say) change in the farmland bird population can involve a large absolute change or a small absolute change, depending on the prevailing local density of birds. Figure 4.4 shows the spatial distribution of farmland birds within each state. In Wisconsin the distribution of farm bird density largely resembles the distribution of agricultural land, being generally high except within a cluster of eight counties in the middle of the state. However, the two distributions are not completely parallel and the area of largest population decrease under the carbon sequestration policy extends well beyond these less intensively farmed counties (Figure 4.4). Since these changes occurred over counties different in area and with different farmland bird densities, a state-wide estimate of farmland bird loss required appropriate weighting of these effects, yielding a net reduction of 11.7 percent for Wisconsin (Table 4.1).

In South Carolina, farmland bird densities increased from the coast to the mountains rather than varying from county to county in direct proportion to the intensity of agriculture in each (Figure 4.4). The gradient was relatively shallow, however, and as a result the changes in farmland bird distribution were largely determined by the relative change in agricultural land: three of the four counties with greatest change in farmland birds—McCormack, Fairfield, and Berkeley—were also among the top four for relative loss of agricultural land, and the patterns of change in agricultural land and in farmland bird distribution were generally similar (compare Figures 4.1 and 4.4). Weighting these

Figure 4.4. Current distribution of farmland bird abundance (left) and projected change in farmland bird abundance under a carbon sequestration policy (right) in southern Wisconsin, South Carolina, and Maine. The metric I is Yang et al.'s (1995) index of total bird abundance across multiple species (see text for details).



Farmland bird abundance

Decrease in farmland bird abundance

Table 4.1. Summary of percentage changes in forest and agricultural land area and in population size of forest and farmland birds.

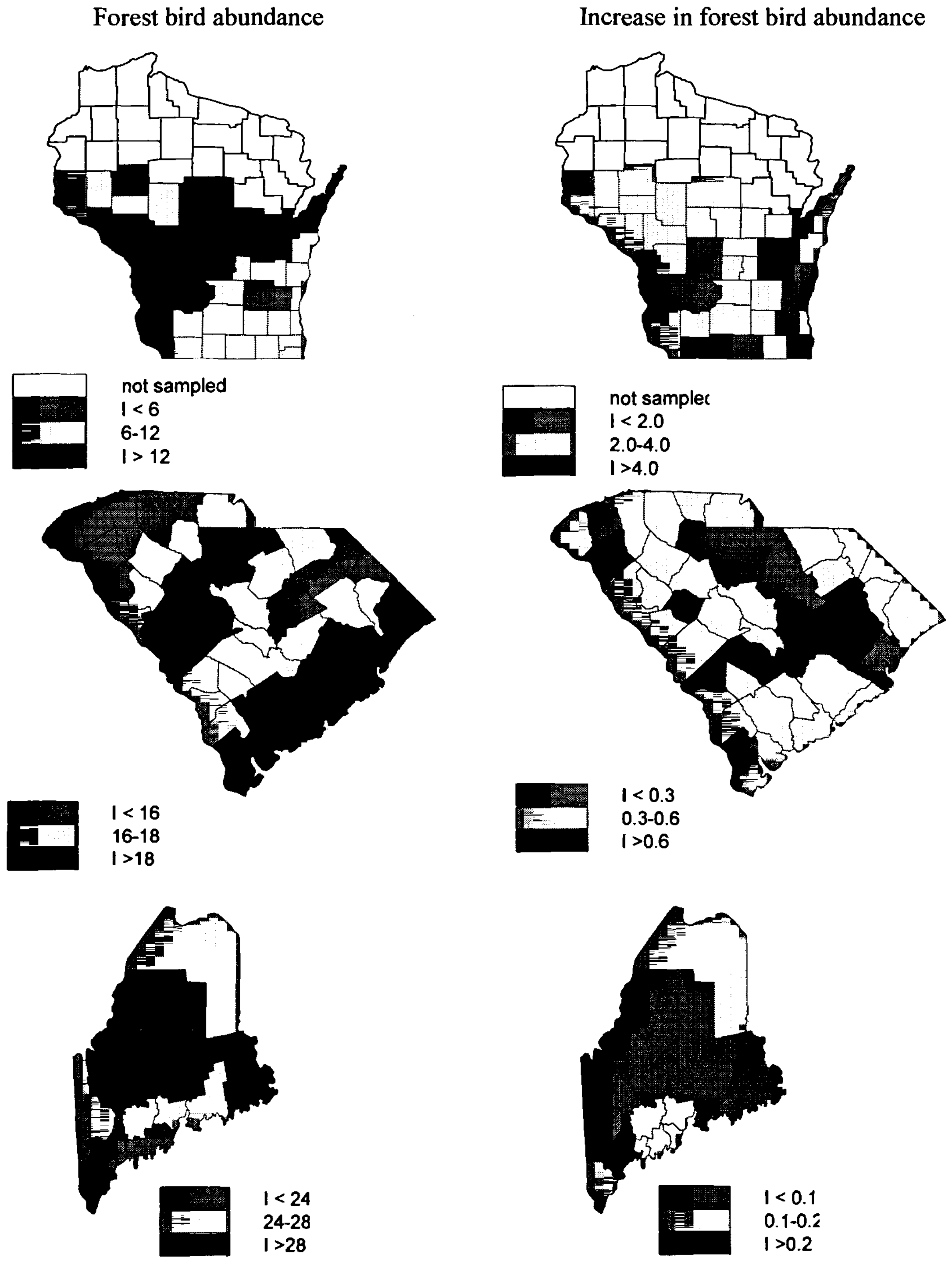
Category	Maine	South Carolina	Wisconsin
		Percentage Changes	
Forestland area	0.3	2.8	18.0
Agricultural land area	-10.0	-10.0	-10.0
Forest birds	3.2	2.5	21.8
Farmland birds	-10.8	-12.2	-11.7
Forest and farmland birds	-2.0	-2.3	-1.1

changes by area and size of current bird population for each county gave a state-wide reduction of 12.2 percent for South Carolina.

In Maine, bird abundance generally decreases from south to north (Allen and O'Connor 2000) and farmland birds, although largely paralleling the distribution of agricultural land, were correspondingly more abundant in southern farming counties than in northern ones (Figure 4.4). As with South Carolina, the gradient was relatively shallow and the changes in bird numbers largely reflected the changes in agricultural land area. When weighted for county area and distribution, the estimate of the state-wide decline was 10.8 percent.

Figure 4.5 shows how the forest bird distribution would change under a carbon sequestration policy. In Wisconsin, the forest bird distribution largely matches that of forests and the largest increases are in counties with proportionately large increases in forest land. However, with dense populations of forest birds across the northwest of the state, even modest increase in forest lands there result in large numerical increase (Figure 4.5). When this is coupled with the large amount of agricultural land available for conversion under the 10 percent scenario, the state-wide increase in forest birds is very substantial, constituting a net increase of 22 percent (Table 4.1). In South Carolina the distribution of forest birds is strongly regional, with highest densities in the Coastal Plain and in the Piedmont, but as there would be relatively little increase in forest area in these parts of the state under the carbon policy scenario, these areas would contribute little to the state-wide population change. Instead, the largest change in forest bird abundance would be across the Atlantic Flatlands but, as forest bird densities there are currently rather low, the increases are also low. As a result, when weighted for area and bird

Figure 4.5. Current distribution of forest bird abundance (left) and projected change in forest bird abundance under a carbon sequestration policy (right) in southern Wisconsin, South Carolina, and Maine. The metric I is Yang et al.'s (1995) index of total bird abundance across multiple species (see text for details).


Forest bird abundance

Increase in forest bird abundance

abundance, the state-wide change in forest bird populations would be only 2.5 percent under the carbon sequestration policy. Similarly, in Maine, despite high densities of forest birds in the North Woods, the planting of additional forest within the extant farming areas results in only minor increases among forest birds (Figure 4.5), with a negligible state-wide increase of 0.3 percent.

4.4.3 Overall bird population changes

Since the loss of agricultural land as habitat leads to a reduction in the farmland bird population in each county while the planting of new forest leads to a gain in forest birds, the net change in bird numbers is a weighted function of the farmland and forest bird densities. Since the area changing in land use and farmland and forest bird densities all vary from county to county, the figures have to be computed within counties and summed to a state-wide total (Table 4.1). In fact, all three states experience a net loss of birds: Wisconsin loses 1.5 percent, South Carolina 2.3 percent, and Maine 2.0 percent. That there should be a net loss even in Wisconsin where the forest bird populations increased disproportionately largely reflects the higher densities of farmland than of forest species.

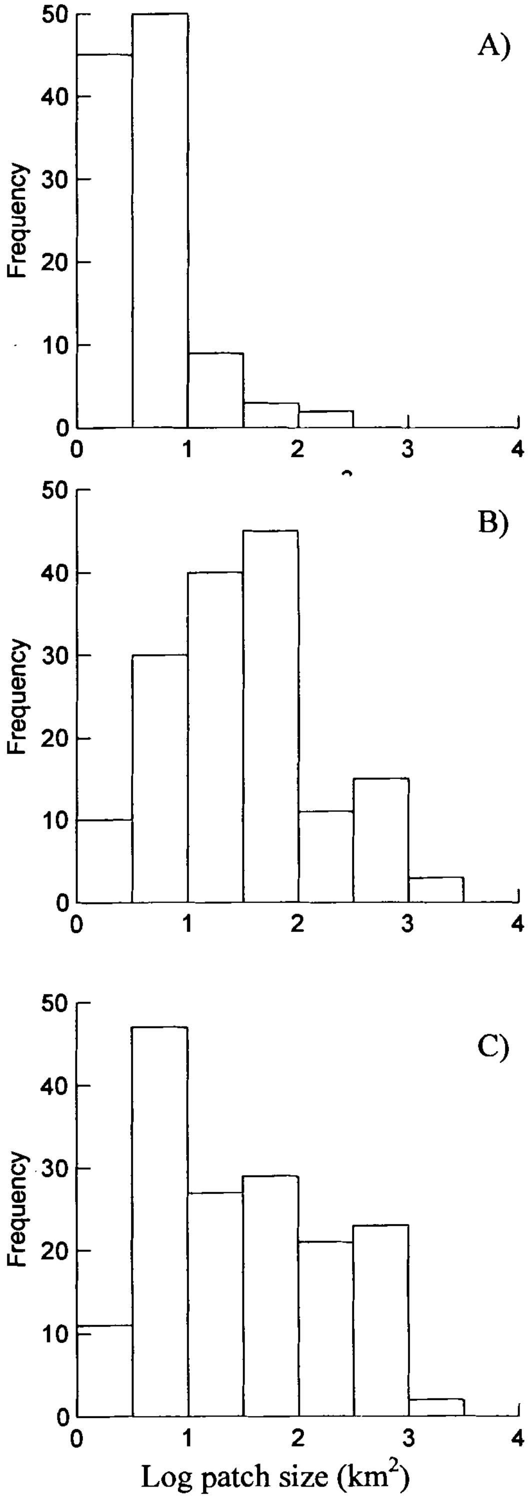
4.4.4 Influence of forest patch size

In calculating the likely effects of afforestation on the populations of forest birds it was assumed above that new planting within any county would induce only a pro rata increase in the local population of forest birds. Where existing forest is distributed as a mosaic of small woodland blocks, however, new planting may coalesce these patches into larger stands of forest. Substantial evidence (Ambuel and Temple 1983, Lynch and Whigham 1984, Askins 1993, Hoover et al. 1995) exists to indicate that bird densities are often very much lower in small patches of forest than in large ones (principally because predators and brood parasites from the surrounding matrix can penetrate a greater proportion of small than of large patches). Whilst much of the evidence derives from small patches some tens of hectares in size, we (R. J. O'Connor and L. Hayes in preparation) have estimated the population losses associated with breeding in forest stands of even some square kilometers (rather than larger ones) to range from 10 to 30 percent for several neotropical migrant bird species. In Figure 4.6, therefore, we show the size distribution of the commonest forest patch types in the three states, as derived from the remotely sensed data used by O'Connor et al. (1996). These data suggest that forest patch sizes in Maine and in South Carolina are generally so large that patch size is unlikely to be a major source of further gain in forest bird numbers. In Wisconsin, forest patches are much smaller and the gains in forest bird populations estimated here for Wisconsin are therefore likely to be minima, possibly to be increased by as much as 30 percent by contiguous planting if the forest species there are generally area-sensitive. At present this is not known.

4.5 Discussion

To the extent possible, all relevant costs and benefits should be considered in developing a national carbon sequestration strategy. Earlier economic analyses of carbon sequestration programs have focused on the opportunity costs of agricultural production, but fail to account for potential environmental effects of afforestation. In this study, we take a first step towards integrating biodiversity impacts into the analysis. The principal value of the results presented here is in their quantification of factors readily identifiable a priori as potentially influencing the biodiversity consequences of carbon sequestration

Figure 4.6. Frequency distributions of forest patch sizes for mixed coniferous-deciduous forests within cells of a 640 km^2 hexagonal grid across A) southern Wisconsin, B) South Carolina, and C) Maine.



policy. These included spatial variation in the density of forest and farmland birds, the relative extent of agricultural land and forest cover within each county, and the relative abundances of the farmland species lost by land conversion to the forest species gained in the newly afforested habitat.

Just as one could anticipate on economic grounds that the conversion of 10 percent of a state's agricultural land to forest is unlikely to result in a constant conversion rate across counties, one could anticipate on biological grounds that bird densities were likely to differ across counties, introducing a spatial component to the pattern of change. The magnitude of this variation across counties proved to be quite substantial (Figure 4.3) and also to have marked spatial patterning (Figures 4.4 and 4.5). These results thus suggest that the biodiversity consequences of afforestation as a carbon sequestration policy are unlikely ever to be captured by simple pro-rating of constant densities to the projected land changes. Moreover, particularly striking in Figure 4.3 is the variation in relative abundance of forest and farmland bird within the three states. The densities of forest and farmland birds clearly respond differentially to variation in environment between regions, and do so by quite significant amounts.

The relative abundance of forest and agricultural land cover within a county influences the relative impact of population changes among forest birds. In each county a particular area of land would convert from crops or pasture to forestry, and with a constant density of farmland birds within a county (assumed here) the relative change in farmland bird populations is then necessarily pro rata. However, the relative effect on the forest bird population in the county is then weighted by the ratio of agricultural land to forest in the county. With twice as much agricultural land as forest, a ten percent loss of agricultural land yields a 20 percent increase in forest, with associated increase in the local forest bird population. And the converse applies.

Whether these land-use changes yield a net increase or decrease in bird numbers also depends on the ratio of the local densities of farmland and of forest birds in the county. Even if a 10 percent change in agricultural land yielded a 20 percent increase in the area of forest, as in the example in the previous paragraph, a net loss of birds results unless the density of forest birds is at least 75 percent that on agricultural land (since a 20 percent increase on 75 yields 90, the reduced density of farmland birds). It is this effect that accounts for much of the net loss in bird numbers that our three study states would experience under the carbon sequestration policy modeled here. This is actually quite counter-intuitive, in that common wisdom holds that loss and fragmentation of forest is a major conservation issue for birds, and it is unexpected to find fewer birds present after planting new forest! It appears that the density of birds on agricultural land may be higher in some states than is commonly acknowledged. Thus, both the relative densities of farmland and forest birds and the relative extent of agricultural land and forest in the county determine whether the policy would result in a gain or loss of avian abundance, with the spatial variation between counties then determining both the spatial patterning of the gains and losses and, by virtue of the variation in area among the counties, whether the state-wide outcome is a gain or a loss.

No consideration was given above to uncertainties in the measurement of the land cover proportions and bird densities, but we expect the uncertainties in our estimates to be small. The base land-use statistics are measured with very little error. The forest area measures are from U.S. Forest Service plot-level surveys, which have relatively small sampling errors. For example, the sampling error for timberland area in most Wisconsin counties (1996 inventory) is below 5 percent. The agricultural land area measures are from the Census of Agriculture, which attempts to provide a complete enumeration of the farm population. Response rates for the Census are very high and, thus, measurement errors are expected to be low. A second source of uncertainty arises with the predictions of land use change. We do not expect the prediction error to be large because of the good fit of the econometric models and the fact that we consider modest changes in land use.

For bird densities the effects of uncertainty in incidence could be assessed by bootstrap sampling of the calculations, but a crude estimate suffices to show that the effect is small. Uncertainty in incidence at a single location will be maximal for a species present in only half the surveys, which with our decadal estimate corresponds to a standard deviation of 0.158 ($=(0.5\text{x}0.5/10)^{1/2}$). If only 40 species (about half of the farmland or forest bird species pools) were present in a location, the standard error for the farmland or forest bird incidence would then be only 0.025, negligible as a fraction of any of the incidences reported in Table 4.1 and an order of magnitude smaller than the changes in overall populations discussed. In practice the use by Yang et al. (1995) of data from multiple locations, the smaller standard deviations of uncertainty in both common and rare species, and the generally larger species tallies at each location mean that census uncertainties can be neglected here.

We noted above that the predictions of forest bird changes might require modification to take account of forest patch size distribution, particularly in Wisconsin. Askins (1993) found that previously declining neotropical migrant species increased in numbers as afforestation restored the contiguity of forest in Connecticut. Hence, our

Wisconsin estimates of the increase in forest bird populations must be seen as conservative: our unpublished estimates indicate that populations of neotropical migrants may be 30 percent lower in areas of forest fragments than where the forest is contiguous. If this were true of the Wisconsin forest species, forest populations could potentially increase by an additional 43 percent (=100/(100-30)) if the new forests were planted to maximize contiguity and reduce patch edge predation and parasitism.

A further assumption in our calculations was that there were no threshold effects in the influence of forest density on birds. It is in principle possible that there might need to be some minimum density of forest in an area before a forest species would settle there, and such an effect would mean that newly forested land in counties with little or no previous forest planting might not yield the expected gain in forest birds. However, the density estimates for forest species that we used were estimated from empirical bird distribution data by Yang et al. (1995) using a grid of sufficient resolution to average four points per county. Accordingly, it is likely that any such effects present have already been incorporated into our analysis.

Our estimates of bird abundance were obtained by summing estimates of incidence—the proportion of surveys at a site that recorded the species—over the 1981-90 decade. It is well established that incidence is directly proportional to absolute densities where estimates of both have been available, except for a small number of very common ubiquitous species whose densities may vary within an incidence of 1.0 (O'Connor and Shrubb 1986, Hanski 1997). If the constant of proportionality were the same for all species, our sum of incidence values for forest species and for farmland species would be directly proportional to the sum of the corresponding bird densities and if the value of the constant were known we could re-express our measure as true densities. It is, however, unlikely that all species share the same constant and this leaves us with a possible bias. Our sum of incidence measure would then really be of form $\Sigma k_i D_i$, where D_i is the density of the *i*th species and k_i is the constant of proportionality between incidence and density for that species. Hence, were the constant for some particular species to be markedly higher than for the other species, then our summed incidence metric would be higher for all points within the range of that species than it should be for proportionality to true total density. However, our metric was summed over many forest and farmland species, so any single error would be relatively small in effect: with 50 species, even a doubling of the constant of proportionality for one species would induce an error of just two parts in a hundred. In addition, with so many species individual errors were likely to cancel each other. We, therefore, consider the likely magnitude of any error from this source to be rather small relative to the effects measured.

One important issue not considered explicitly here is that different species have different conservation significance. Our present calculations treated all species as equally important and computed the net change in birds under a carbon sequestration policy as the sum of the forest and farmland bird changes in a county. In practice, some of the species lost from the newly forested agricultural land will be of greater conservation value than the forest species gained. In principle, the analysis presented here could be conducted using an index of conservation value instead of the incidence metric. For example, the incidence value for each species in a county could be weighted to reflect its relative conservation value, and the calculations that were here applied to just two groups—total forest birds and total farmland birds—could instead be computed over each of the entries in vectors of individual species incidence values for forest and for agricultural land. Applying the conservation weights to the results with and without the sequestration policy would then yield estimates of the magnitude and distribution of conservation impacts. Several of the conservation value weighting schemes devised for biodiversity complementarity analyses (Polasky and Solow 1995, Csuti et al. 1997) could readily be adopted for use in the present context. As well, willingness-to-pay estimates from non-market valuation studies could be applied to derive explicit estimates of the benefits or costs associated with changes in bird populations.

As noted above, carbon sequestration is the objective of the policy considered in this study and the scenario we evaluate is designed to achieve a given level of land enrollment at the least cost. There are several ways in which biodiversity impacts—and other environmental effects of afforestation—can be incorporated into the analysis of carbon sequestration policy. If estimates of all the relevant benefits are available, including the benefits of climate change mitigation and biodiversity, then a standard cost-benefit analysis can be performed. In this case, the optimal policy is to enroll land until the marginal cost of enrollment equals the sum of marginal benefits.[7] If, as in the present case, reliable benefits estimates are elusive because of the complexities of the natural phenomenon involved, an alternative is to conduct cost-effectiveness analysis. This might involve minimizing the total cost of enrolling land subject to constraints on the

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[7] For a given amount of land conversion, the marginal cost of enrollment equals the corresponding per-acre subsidy that is used in the simulations. The marginal cost of enrollment reflects the opportunity cost of agricultural production. See Plantinga et al. (1999) for more details.

minimum amount of carbon sequestered and the maximum tolerable impacts on biodiversity. Assuming the biodiversity constraint binds, the solution identifies the cost of departing from a least-cost carbon sequestration strategy in order to accommodate biodiversity objectives. The shadow value on the constraint gives the implicit price for biodiversity and, thus, sheds light on the nature of the tradeoffs involved.

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