Geographic Location and Ecoregional Effects on Determinants of Avian Species Richness

by
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Geographic Location and Ecoregional Effects on Determinants of Avian Species Richness

Abstract: *Biodiversity studies allow for a more holistic approach to the conservation of species. Using one measure of biodiversity, that of species richness, this study investigates the correlations between bird species richness and a set of variables. These variables represent climate, productivity/available energy, habitat heterogeneity, disturbance, and topography. Another aspect of this study is to group the data contained within equal-area hexagons according to two levels of organization. The large scope organized hexagons into the West Coast region and Chesapeake region. At the small scope, there were five groupings according to ecoregions within each of the larger regions. The resulting models show that differences in significant variables occur between regions and each ecoregion. These determinants of bird species richness vary between the two regions because climate, landscape structure, and topography are processes that are acting differently to shape the distributions in richness. Determinants also vary between each of the ecoregion groups because these same processes producing different richness patterns. Further emphasized by this study is the importance of acknowledging the connectivity between ecosystems and species, this being important for the management and conservation of bird species richness.*

Table of Contents

Page

List of Figures

List of Tables

Geographic Location and Ecoregional Effects on Determinants of Avian Species Richness

Introduction

Biodiversity

Biodiversity spans the fields of biogeography, botany, conservation biology, ecology, genetics, palaeontology, systematics, and zoology. Some view biodiversity as a concept, others as a measurable entity, and still others view the term as a political or social construct. Despite its vagueness, biodiversity as a concept has led the scientific community to focus on such questions as: How many species of plants and animals exist and where? How do diversity and processes interact? Which biological groups are functionally more important (Gaston 1996)?

The importance of biodiversity developed out of the value that society places on species. To some, species carry intrinsic value (Callicot 1986; Ehrlich and Ehrlich 1992; Kunin and Lawton 1996). Therefore, diversity is an issue due to increasing losses to extinction. Biodiversity studies are a call to address issues holistically, rather than the traditional species by species method of conservation (Noss 1990).

Measuring biodiversity

Several schemes have been developed to capture the broad scope of biodiversity, and to make sense of the 'variety of life'. These schemes serve as a construct by which the many features of biodiversity can be measured (Gaston 1996). Two schemes stand out in the literature. One classification distinguishes between genetic diversity, species or taxonomic diversity, and ecosystem diversity (McAllister 1991). Another classification distinguishes between structural level, compositional level, and functional level (Franklin et al. 1981; built upon by Noss 1990). Regardless of which scheme is used, there is a hierarchical nature to approaching biodiversity (Norton 1994; White et al. 1999).

This hierarchical nature implies that assessment and monitoring of biodiversity must be at multiple levels of organization, and multiple spatial and temporal scales (Noss 1990; White et al. 1999). Ecological systems tend to "generally show characteristic variability on a range of spatial, temporal, and organizational scales (Levin 1992)." The significance of levels and scales depends on the questions of interest.

Species Richness as a measure of biodiversity

Because of its hierarchical nature, a single measure cannot capture biodiversity. Species richness is one useful and widely accepted measure. It is defined as a count of species in an area. Species richness is capable of capturing the diversity of life as represented by a count of species, but is unable to determine within species diversity. It cannot answer the question of how related two species might be, or the question of their functional diversity (Gaston 1996). Focusing on the species level is more practical and serves as a surrogate for genetic diversity (White et al. 1999). This project investigates one part of biodiversity research, that of avian species richness. It is intended that the findings of this project contribute to the understanding of patterns of biodiversity.

Spatial Patterning of species richness

The spatial patterning of biodiversity and the variety of life is reflected in part by the distribution of species richness. Also, spatial patterning captures other facets of this variety. Underlying the patterns of species richness are processes. Pattern is observable, but process is more difficult to detect (Brown 1995; Levin 1992). Patterns of species richness are useful for prioritization in conservation efforts. Spatial patterns are also important to the assessment and management of risk to species (White et al. 1999).

Relating species richness to environmental variables

Studies of the relationships between species richness and environmental determinants have been numerous (Abramsky and Rosenzweig 1983; Turner et al. 1987; Currie 1991; Wright et al., 1993). Also, there are several studies of bird species richness as related to environmental determinants (MacArthur 1964; Recher 1969; Rabinovich and Rapoport 1975; O'Connor et al. 1996; Bohning-Gaese 1997; White et al. 1999).

These studies are driven by the desire to understand the determinants of species richness, but more currently to understand the driving processes forming the patterns we see in species richness for conservation purposes (Gaston 1996). Despite the long years of study, there are similarities in the findings. Similarities exist in the processes acting to form the patterns of bird species richness.

By knowing which processes are creating these patterns, perhaps we are then able to predict species richness in areas where it may be unknown. Another purpose for knowing processes forming these patterns is for prediction of future events or scenarios, such as loss of habitat and global climate changes. Being able to predict the consequences is a major step in risk management and conservation efforts.

This project further investigates some determinants correlated with bird species richness. Using an *a priori* knowledge of hypothesized determinants, a set of variables were chosen to test their relatedness to bird species richness. The variables significant in predicting species richness were found for two levels of grouping the study units to be discussed in the following section.

Issue of spatial scale

As Weins describes, "scaling issues are fundamental to all ecological investigations (1989)." In attempts to understand ecological systems, it has become evident that pattern and process are highly scale dependent. It is suggested that pattern and explanations of pattern will change with spatial and temporal scale (Levin 1992; O'Neill 1995). For purposes of investigating ecological systems or populations, there is no universally relevant scale. It depends upon the inquiry of interest (Allen and Starr 1982; Weins 1989; Levin 1992).

As the literature suggests, different patterns of species richness are elucidated at different scales (Wiens 1989; Stoms 1994). Differences in patterns and environmental correlations found between scales are due to differences in scale (Diamond 1988; Stoms 1994). Similarly, by changing the groupings of study units, as done in this study, different environmental correlates of the groupings were elucidated. The two "groups" of interest are that of the ecoregion level and that of geographic region within the US.

Study units are (1) grouped by geographic region located within the U.S., herein referred to as large scope. Study units are also (2) subdivided according to which ecoregion they fall within, herein referred to as small scope. More specifically what is suggested is that determinants found to be significant in predicting species richness for individual ecoregions differ amongst one another, and differ from the larger scope determinants of the geographic region. If the explanations and predictors of patterns do differ, this further reinforces the idea that the scaling issue is significant to ecological investigation.

At the large scope, the two geographic regions of interest are the West coast region made up of three states, and the Chesapeake region made up of five states (to be discussed in the methods section). Differences in these significant explanatory variables might suggest that different ecological and evolutionary processes are acting to produce different patterns of species richness in the two geographic locations of interest.

At the smaller scope, study units are grouped according to ecoregion delineation. For the purposes of this study, Level II ecoregions of North America developed by the Commission for Environmental Cooperation was chosen (CEC, 1997). According to Omernik, ecoregions are based on "perceived patterns of a combination of causal and integrative factors including land use, land surface form, potential natural vegetation, and soils" (Omernik 1987, p. 118). They are a general delineation of areas of similar ecosystems. Expanding on the idea that resources are generally similar within ecoregions, it might also be suggested that because of ecoregional differences, the processes involved in forming patterns of species richness also differ across ecoregions.

Objectives

There are two main goals of this research. The first goal is to determine variables to predict distributions of existing bird species richness. The second goal of this research is to identify differences that exist between predictors of species richness at the two scopes discussed previously. Also, part of this goal is to determine differences in predictors between the two geographic regions. These goals are accomplished by the following objectives:

1. Group data (study units) according to geographic region (the West Coast region or the Chesapeake region).
2. Develop predictive model for bird species richness at the large scope for the two geographic regions.
3. Group data (study units) by ecoregion. Identify groups using a geographical information system (GIS) by overlaying ecoregions with study units.
4. Develop predictive model for bird species richness at the small scope for each of the ecoregions.
5. Compare determinants of bird species richness between the two geographic regions at the large scope, and individual ecoregions at the small scope.
6. Explore relevance of research and discuss further research needs.

Methodology

Study region

Data was obtained for two geographic regions located within the U.S. This data was chosen based on limited availability. In the Chesapeake region, Delaware, Maryland, Pennsylvania, Virginia, and West Virginia are included. Washington, Oregon, and California in the West Coast region are also included. These locations are depicted in Figure 1.

Ecoregions falling within these two regions are to be considered. Level II ecoregions, of which there are 52 classes for the continent will be overlayed with the study units. Table 1 is a list of the involved ecoregions. Figure 2 illustrates locations of relevant ecoregions.

Units of study

The study units from which the models will be developed are hexagons approximately 640 square kilometers in area. These hexagons make up a grid, which covers the two geographic regions of interest (see Figure 1). Data for bird species richness and all environmental determinants are contained within and generalized for each hexagon (study unit). A total of 1992 hexagons are used for the analysis. Of this total, 1437 hexagons make up the grid covering the West coast region, and 555 hexagons make up the grid covering the Chesapeake region.

For the purposes of environmental monitoring and assessment, a grid of hexagons such as this is a suggested spatial framework from which to work. It is recommended for providing a regular, systematic, hierarchical spatial structure for analyses. The purpose of using such a framework is for having a set of single units for comparing large amounts of data. Locations of species are generalized so as to account for the uncertainty of occurrence. And, an equal-area sampling grid is used for the purpose of avoiding

West Coast and Chesapeake Region Locations

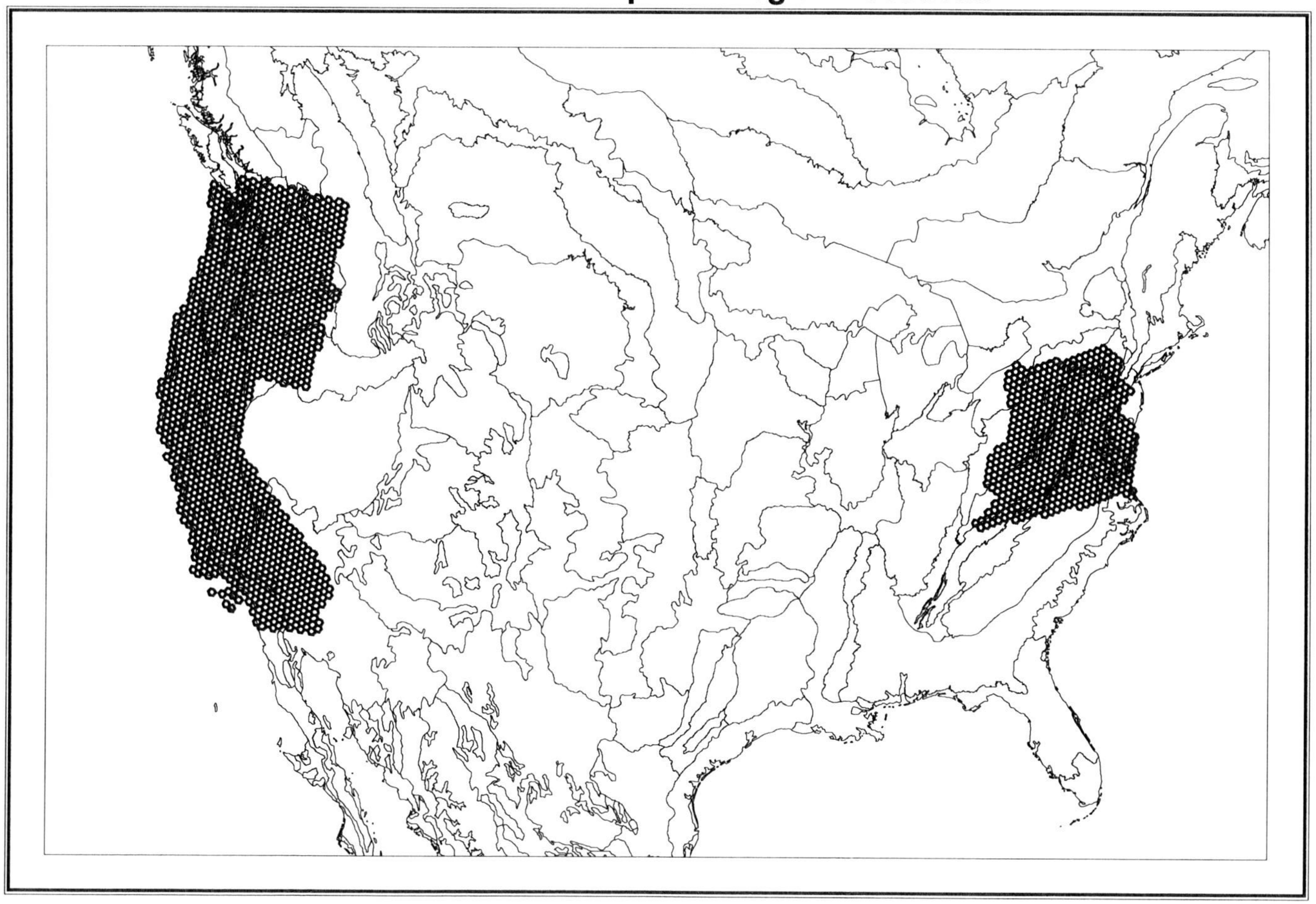


Fig. 1. The West coast region illustrated above is made up of Washington, Oregon, and California. The Chesapeake region consists of Deleware, Maryland, Pennsylvania, Virginia, and West Virginia. The grid of hexagons overlaying these ecoregion boundaries are the study units. Each hexagon is 640 square kilometers.

Table 1 There are five ecoregions falling partially or completely in both the (a) West Coast region and the (b) Chesapeake region. The ecoregion numbers listed correspond with the labels in the next illustration (Figure 2). Ecoregion boundaries are used to group the hexagons for regression model building at a smaller scope.

(a) West Coast Region

Ecoregion	Description
6.2	Western Cordillera
7.1	Marine west coast
10.1	Western Interior basin and range
10.2	Sonoran and Mohave deserts
11.1	Mediterranean California

(b) Chesapeake Region

Ecoregion	Description
5.3	Atlantic Highlands
8.1	Mixed Woodland plains
8.3	Southeastern USA plains
8.4	Ozark, Ouachita-Appalachian forests
8.5	Mississippi alluvial and Southeastern coastal plains

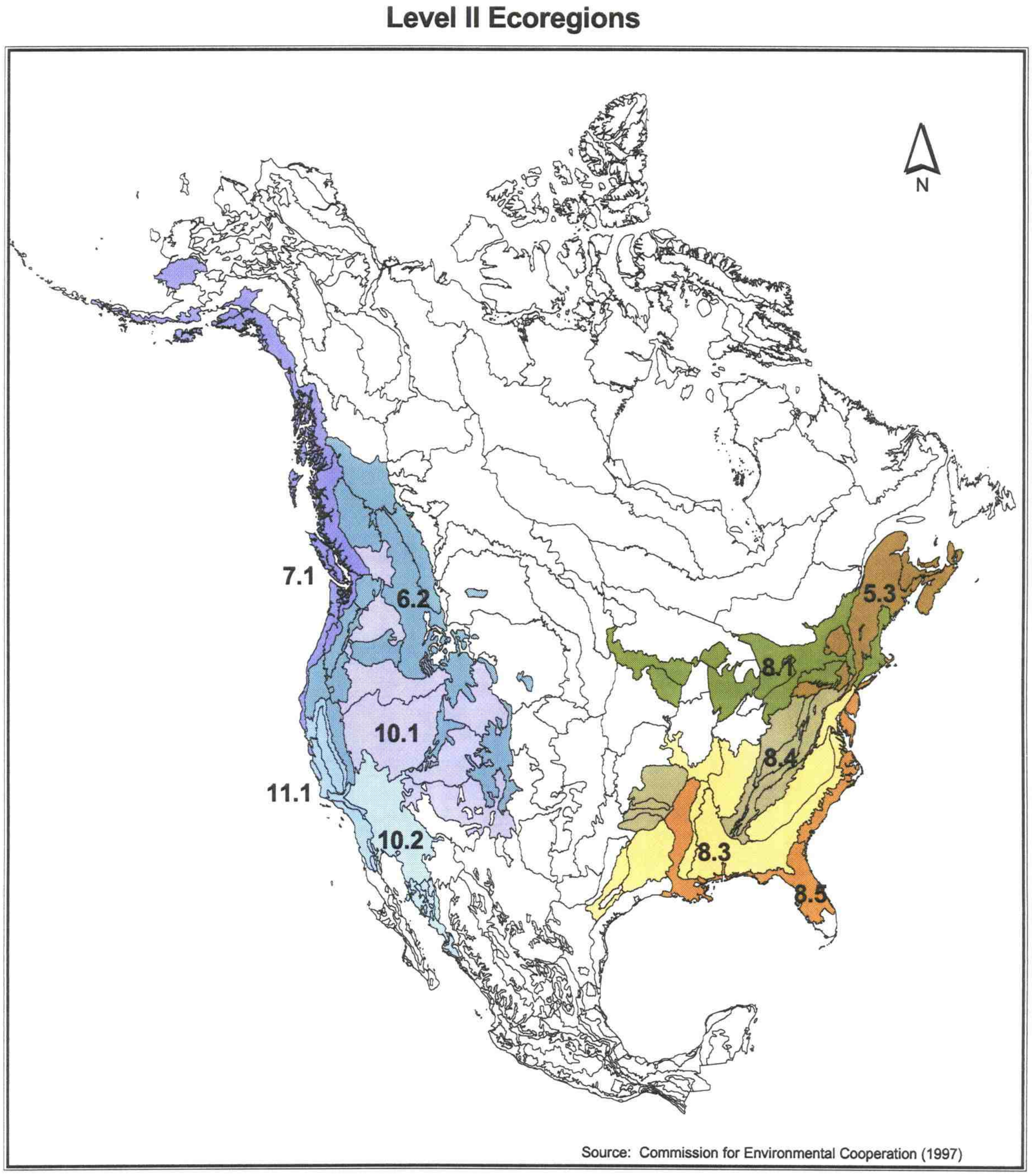


Fig. 2. Illustrate above are the ecoregions involved in this study. Hexagons are grouped according to which ecoregion they fall within. To be included in an ecoregion, the criteria of 50% of the hexagon within the boundary must be met.

confounding analyses (White et al. 1992). It allows for the comparison of data through a means separate from ecological processes, geographic barriers or human defined boundaries.

Response variable

The response or dependent variable used in this study is bird species richness. It is defined here as the number of native summer resident breeding bird species. Each hexagon has a value for this variable. The species level of organization was chosen because of the availability of the data. This level was also chosen because of its usefulness and practicality as a measure of biodiversity. The spatial distribution of bird species richness across both geographic regions is illustrated in Figure 3.

Explanatory variables

Explanatory variables were also selected based on the availability of the data. The explanatory variables from the dataset are listed and described in Table 2. These possible determinants of bird species richness are measures of climate, land-use, landscape patchiness, and elevation. Figure 4 shows examples of their spatial distributions across the two study regions. Explanatory variables fit into the regression models are considered significant in determining the existing patterns bird species richness.

These explanatory variables are also representative of the processes hypothesized to be predictive of bird species richness. As discussed previously, processes such as climate, productivity, topography, habitat heterogeneity, disturbance, and latitudinal gradients have been hypothesized to be indicators of species richness (Kiester 1971; MacArthur 1972; Brown and Gibson 1983; Schmida and Wilson, 1985; Currie 1991; Ricklefs and Schluter 1993; Wickham et al.1997). Table 3 summarizes these suspected processes, and indicates which explanatory variables from the dataset are representative

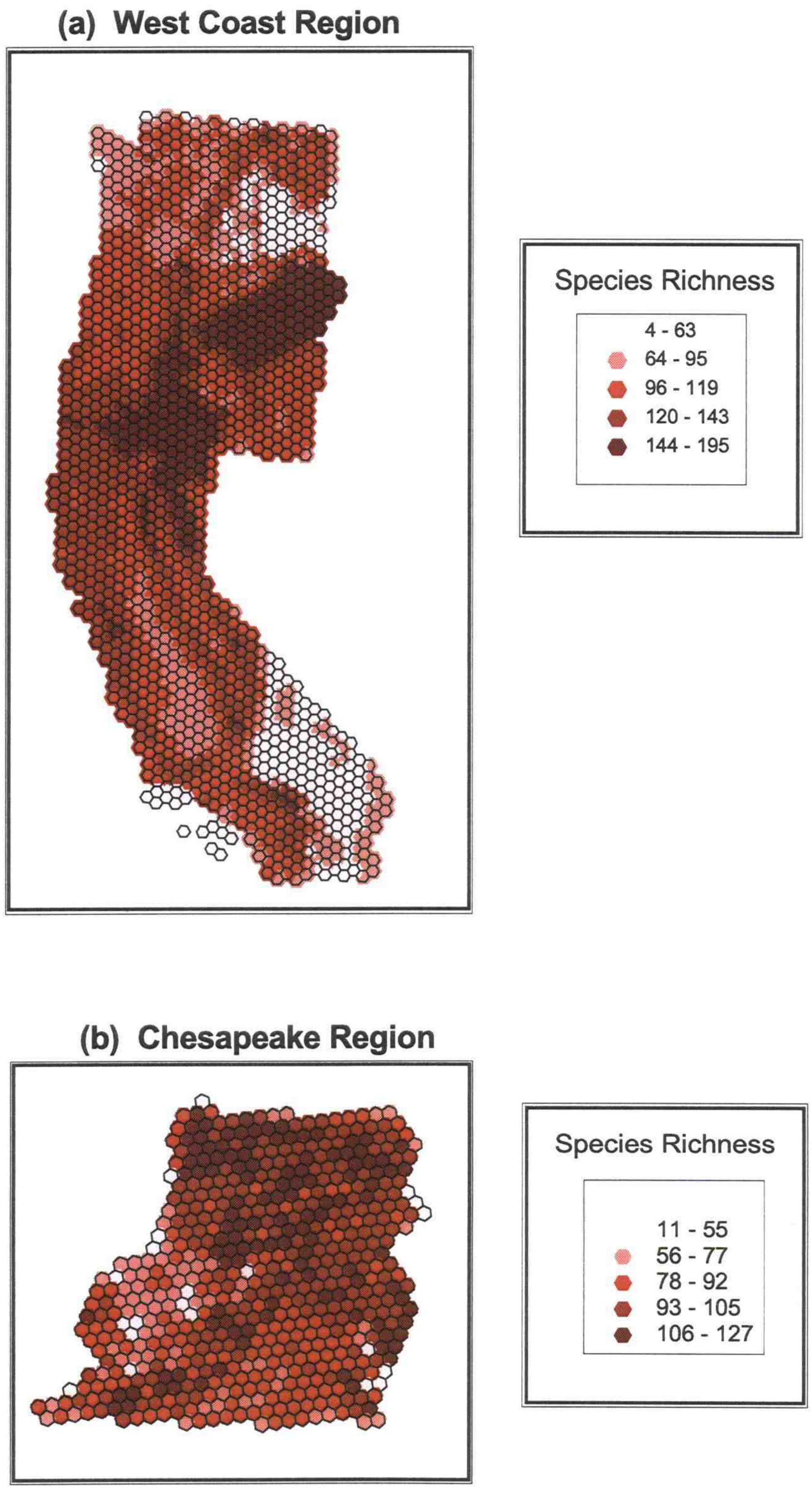


Fig. 3. Illustrated are the species richness distributions for the (a) West coast and (b) Chesapeake regions of this study.

Table 2 The following is a list of variables in the datasets. The dependent variable and some of the explanatory variables were used in building regression models for the regions and ecoregions. Variables were not used if only zero values existed for a particular grouping. The first column is an abbreviation of the variables. The second column contains a short description of the variables.

Dependent Variable	**Description**
Birdspp	Bird species richness

Explanatory Variable	**Description**
JaSd	January temperature, standard deviation (C)
JaMn	January temperature, minimum (C)
JlSd	July temperature, standard deviation (C)
JlMx	July temperature, maximum (C)
PptAvg	Annual precipitation, mean (mm)
PptSd	Annual precipitation, standard deviation (mm)
SeasAvg	July – January temperature, mean (C)
SeasSd	July – January temperature, standard deviation (C)
ElAvg	Elevation, mean (m)
ElSd	Elevation, standard deviation (m)
nlu	# land use classes (range 1-160)
patgt4	# patches, size > 4 pixels
fractal4	Fractal metric, patches of size > 4 pixels
scDOM	Dominance metric
scCON	Contagion metric
lcc1	Area in cropland/pasture mixture (proportion)
lcc2	Area in grassland/cropland mixture (proportion)
lcc3	Area in woodland/cropland mixture (proportion)
lcc4	Area in grass dominated (proportion)
lcc5	Area in shrub dominated rangeland (proportion)
lcc6	Area in mixes (grass/shrub) rangeland (proportion)
lcc7	Area in deciduous forest (proportion)
lcc8	Area in conifer forest (proportion)
lcc9	Area in mixed (deciduous/conifer) forest (proportion)
lcc10	Area in water bodies (proportion)
lcc11	Area in coastal wetlands (proportion)
lcc12	Area in barren or sparsely vegetated (proportion)
lcc13	Area in alpine tundra (proportion)
lcc14	Area in urban area (proportion)
FdTot	Federal land, total (sq km)
RvrTot	Streams, total (km)
RdTot	Roads, total (km)

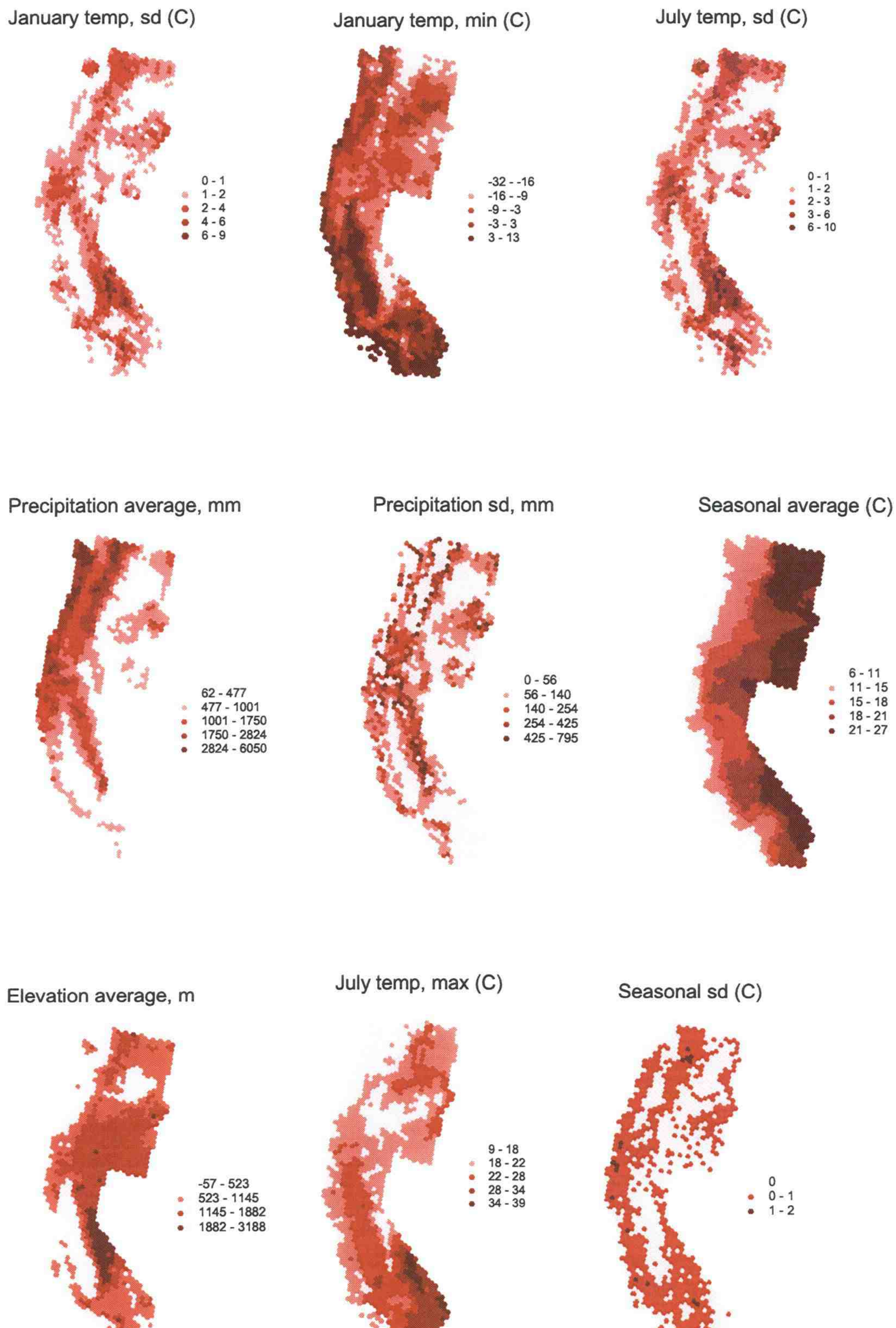


Fig. 4. These are example spatial distributions of explanatory variables over the West Coast and Chesapeake regions.

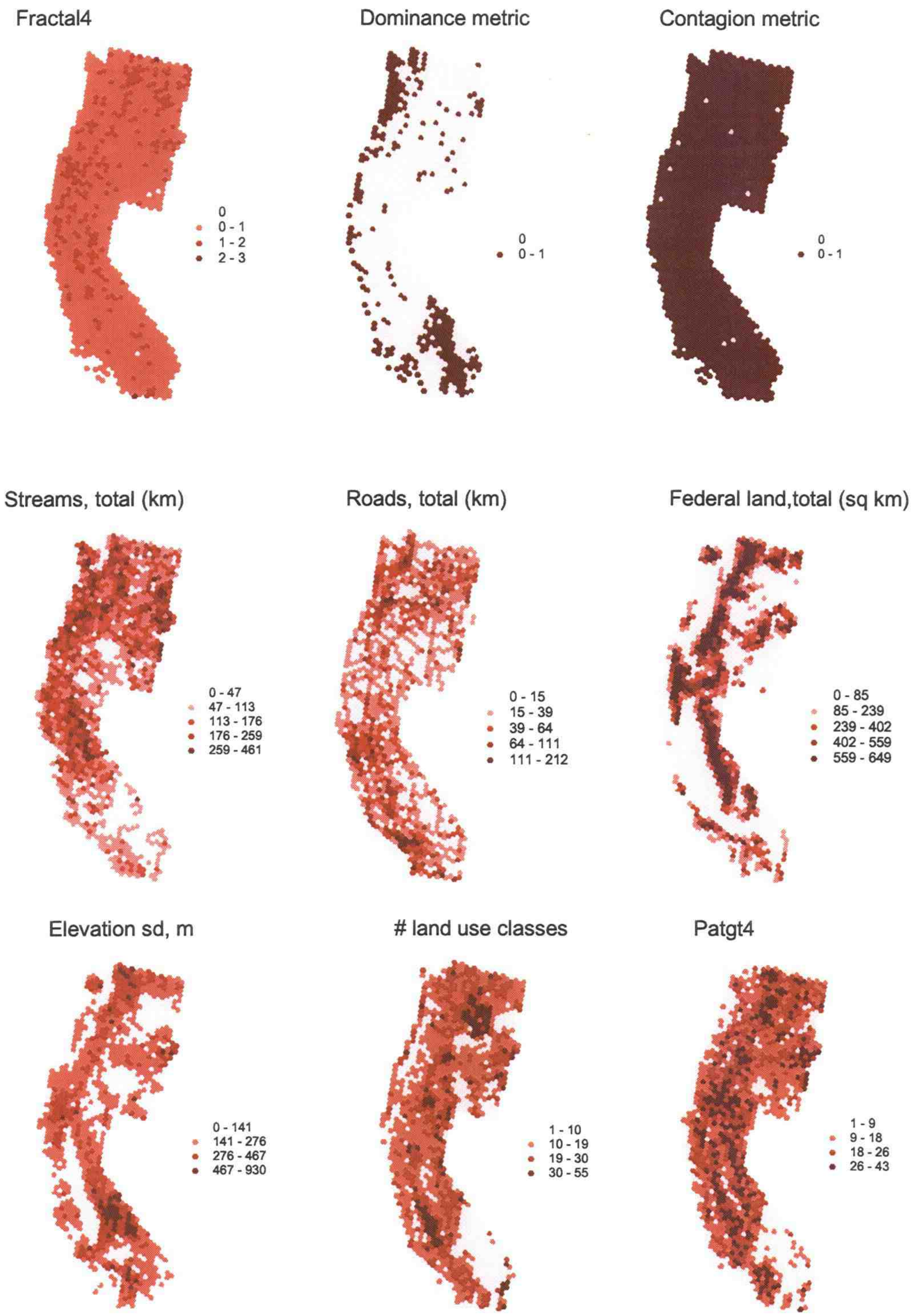


Fig. 4, Continued.

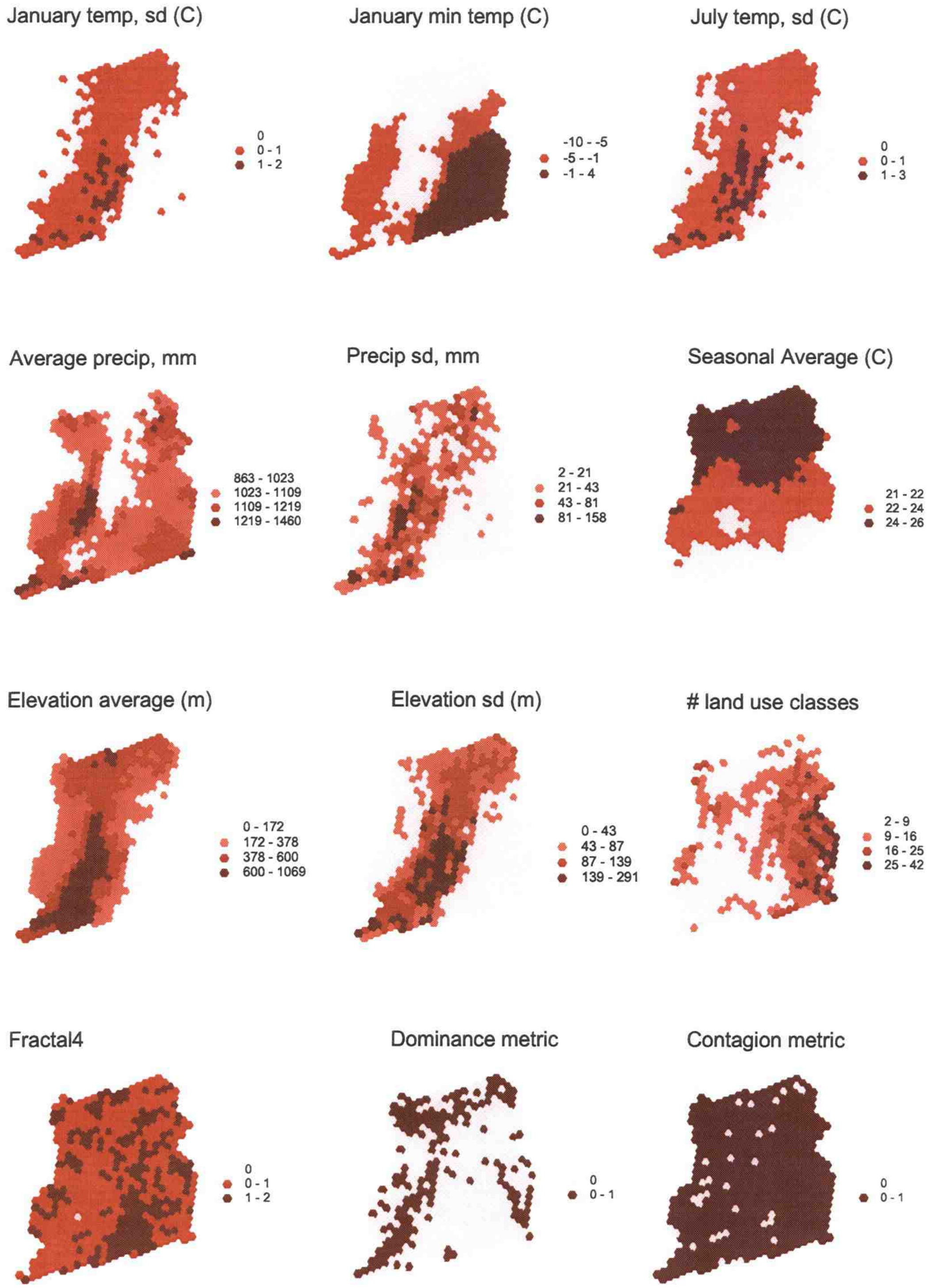


Fig. 4. continued.

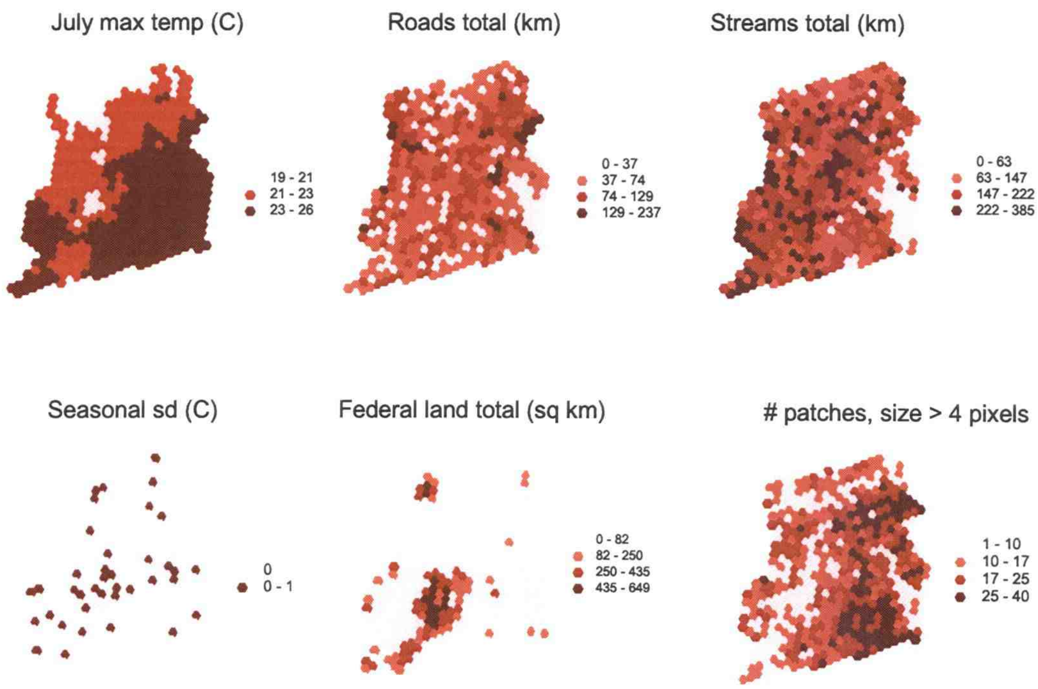


Fig. 4. continued.

Table 3 The first column lists processes thought to be significant in shaping patterns of bird species richness. The list of processes was developed from biogeographic hypotheses explained in the second column. The sources for these hypotheses are also listed. Explanatory variables were used to test the suggested processes. Listed variables appearing in any of the models may be an indication that the corresponding process is influencing the patterns of species richness that exist.

Process	**Hypothesis**	**Source**	**Explanatory Variables**
Climate (stability and extremes)	Also aridity gradient- species decrease with increasing aridity	Brown and Gibson, 1983, Wickham et al., 1997	January temp standard deviation, January temp min, July temp standard deviation, July temp max, annual precipitation mean, annual precipitation standard deviation, seasonal average, seasonal standard deviation.
Productivity/ Available energy	Large scale, species richness increases with increasing available energy or productivity, or it limits species richness	Currie, 1991	Elevation mean, proportion of area in land classes 1-14, streams total
Habitat heterogeneity	Species richness increases with habitat heterogeneity (representative of variability in structure and function and changeability of environment)	Schmida and Wilson, 1985	Number of land use classes, number of patches, fractal metric, dominance metric, contagion metric, proportion of area in land classes 1-14, total federal land
Disturbance	Intermediate stress results often in high species richness	Wickham et al., 1997	Road total
Topography	Species richness decreases with increasing elevation	Ricklefs and Schluter, 1993	Elevation mean, elevation standard deviation

Steps of analysis

In order to accomplish the first two objectives listed in the previous section, the data set is divided according to which geographic region the hexagons belong. Two models were developed at this large scope for bird species richness with the set of explanatory variables using MLR in SAS (statistical package).

Initially, a correlation analysis of all variables was conducted. Correlation coefficients from this analysis along with scatter plots of all variables will be used to determine which variables are highly correlated, and which variables require transformations. Detecting multicolinearity prior to fitting a model reduces bias in the model. The criterion used in this study for the elimination of highly correlated explanatory variables is a correlation coefficient of 0.50 or greater. Elimination of explanatory variables may also be due to only zero values present. Assumptions of normal distribution and equal variance will also be investigated using these results.

Next, multiple linear regression is used to determine relationships of the response variable (bird species richness) and explanatory variables (environmental determinants representing processes). The manual stepwise variable selection approach will be taken using SAS. The criteria for entry and exit of a variable will be the significance level of 0.05 and 0.10, respectively.

Mathematical models will be developed from this analysis describing the relationship of bird species richness with the set of variables:

$$Y_i = \beta_0 + \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \ldots + \beta_p X_{pi} + \epsilon_i$$

where $\epsilon_i \sim N(0, \sigma^2)$ and all ϵ_i's are independent, the β's are the regression coefficients, and where:

Y_i	is the bird species richness in a hexagon cell
X_i	is the p set of explanatory variables of the ith hexagon observation
ϵ_i	is the random effect of each hexagon that adds variability to the value of Y

This third objective of grouping the hexagons according to ecoregions was accomplished through the use of GIS. ArcInfo was used to overlay polygon features of the North American ecoregion coverage with hexagons. Hexagons with 50% or more of their area within an ecoregion boundary were grouped under that ecoregion. Ecoregion groups were eliminated if less than 30 hexagons made up the set. The fourth objective of developing models at the small scope, for each ecoregion, uses the same approach of model development described previously.

The fifth and sixth objectives were accomplished by discussing qualitative differences in predictors of models between geographic regions and between scopes. Caveats and relevance of results will be discussed along with suggestions for further or improved research.

This observational study looks at data for two specific regions in the United States. The scope of inference is narrow. Inferences drawn from this study are limited to native breeding bird species present in these two particular areas of study.

Significance of research

As described before, biodiversity is important. Before the concept of biodiversity carried importance in scientific communities, many past management strategies and assessments focused on saving one species at a time. But, still we lost species to extinction. The emergence of the biodiversity concept in the scientific realm moved the focus of current research to preserving ecological systems as a whole. Preserving not just species, but their interactions and their environments is fundamental to conservation strategy.

Contributions made to these efforts may help prevent endangerment and possible extinctions of species. Studies determining patterns of diversity and correlating them with environmental patterns can be translated into management schemes to protect and conserve species. This research contributes to the concept of biodiversity as a whole. More specifically, this research contributes to the assessment of bird species richness. As one measure of biodiversity, species richness is used as a response variable. By correlating a set of explanatory variables, predictive models of bird species richness can be constructed. In this research, the purpose of the models is to generate discussion of ecoregional differences that may affect patterning of bird species richness, geographical location differences that affect patterning, and spatial scale that may also affect patterning.

Results and discussion

A preliminary analysis of correlation coefficients and scatter-plots led to the elimination of several explanatory variables prior to model building. Explanatory variables were eliminated if only zero values were present or if they were highly correlated with other variables. Thus, the number of explanatory variables entering into regression differed for all groupings. The goal was to simplify and develop models with a set of variables that preclude multicolinearity. Therefore, final models with fewer explanatory variables and lower R-square values are accepted as meaningful. More confidence is places in models with higher R-square values.

Preliminary analyses also resulted in transformations of the data and detection of any outliers. Log_e transformations were taken on some explanatory variables, and sometimes on the response variable, as needed to stabilize variances and linearize relationships with other variables. Residual plots were developed for initial models. Outliers were detected, but all values were kept in the dataset. Also, values were kept for all hexagons regardless of their amount of area over water.

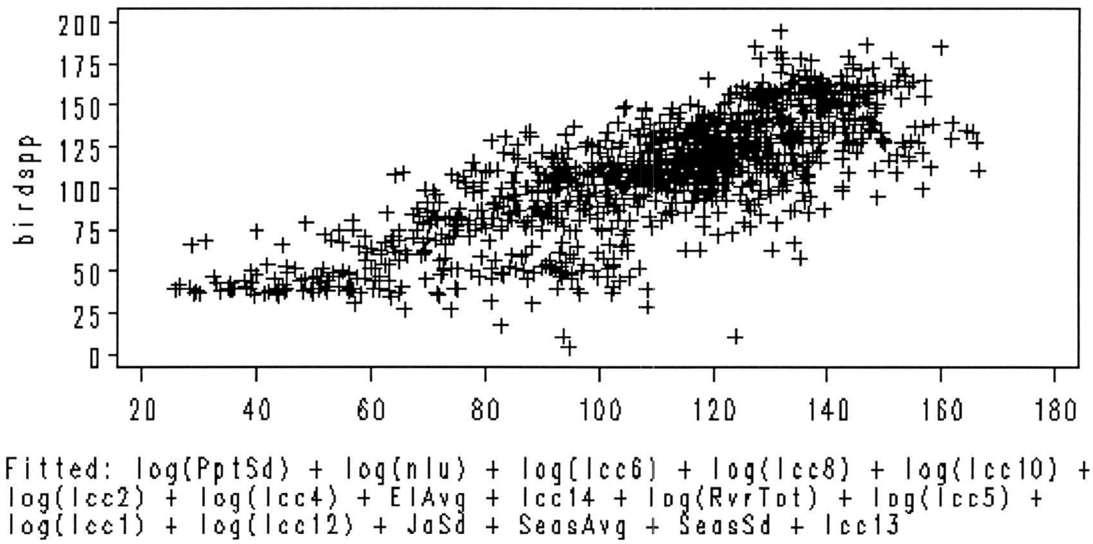
In addition, the number of study units, or hexagons, varied for each region and ecoregion. The number of hexagons used in the regression model building varied from 32 to 1,437. This is important when considering and comparing the models. The regression results are summarized for the West coast region and ecoregions in Table 4, and for the Chesapeake region and ecoregions in Table 5.

Location differences result in differences in models for the two geographic regions of the US used in this study. Landscape patterns differ between these two regions because of the geologic history. Climatic regimes of these two regions create two patterns of vegetation. The human population, and the use of land by humans, which differs between these two regions, also determines landscape patterns. In turn, these differences in climate and landscape pattern are going to affect the bird species richness distributions. As well, the distributions within the ecoregion groupings are going to differ for the same reason.

Table 4 The following are summary tables of the regression results for the (a) West Coast region and (b) its ecoregions. Models are given with regression coefficient standard errors beneath. Also listed are the number of hexagons used in the regression, the R-squared values, adjusted R-squared values, Mallow's Cp statistics, and root mean square errors. The tables illustrate the significance of variables in the model.

(a) West Coast Region Model

Birdspp = -3.201 + 4.7002 lPptSd + 9.0622 lnlu + 100.09 llcc6 + 115.53 llcc8 + 99.201 llcc10 + 112.66 llcc2 +
(11.936) (0.823) (1.174) (13.467) (15.571) (15.233) (14.083)
99.054 llcc4 + 0.0211 ElAvg + 79.88 lcc14 + 2.1921 lRvrTot + 59.467 llcc5 + 67.612 llcc1 + 66.999 llcc12
(13.427) (0.002) (14.312) (0.453) (13.724) (15.573) (14.556)
- 1.9621 JaSd - 1.3306 SeasAvg - 6.3307 SeasSd - 38.779 lcc13
(0.717) (0.218) (2.925) (18.065)



N=1437
R square=0.621
Adjusted R^2=0.615
Cp=18.000
RMSE=21.542

Table 4, Continued

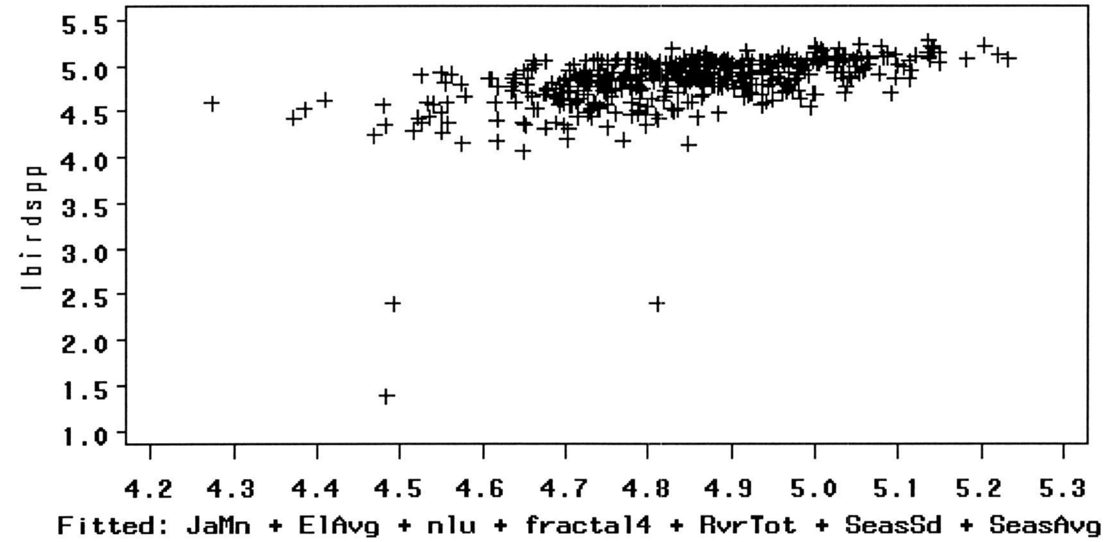
Variables	**Regression Coefficient**	***t***	***P***
Intercept	-3.201	-0.27	0.7886
log(PptSd)	4.7	5.71	<0.0001
log(nlu)	9.062	7.72	<0.0001
log(lcc6)	100.089	7.43	<0.0001
log(lcc8)	115.532	7.42	<0.0001
log(lcc10)	99.201	6.51	<0.0001
log(lcc2)	112.657	8	<0.0001
log(lcc4)	99.054	7.38	<0.0001
ElAvg	0.021	12.43	<0.0001
lcc14	79.88	5.58	<0.0001
log(RvrTot)	2.192	4.84	<0.0001
log(lcc5)	59.467	4.33	<0.0001
log(lcc1)	67.612	4.34	<0.0001
log(lcc12)	66.999	4.6	<0.0001
JaSd	-1.962	-2.74	0.0063
SeasAvg	-1.331	-6.09	<0.0001
SeasSd	-6.331	-2.16	0.0306
lcc13	-38.779	-2.15	0.032

Table 4, Continued

(b) West Coast Ecoregion Models

Ecoregion 6.2 – Western Cordillera

Lbirdspp =
4.4986 +0.0317 JaMn + 0.0002 ElAvg + 0.0082 nlu – 0.1164 fractal4 + 0.0006 RvrTot + 0.0814 SeasSd +
(0.104) (0.003) (0.000) (0.002) (0.027) (0.000) (0.026)
0.0146 SeasAvg
(0.004)



N=495
R square=0.233
Adjusted R^2=0.222
Cp=8.000
RMSE=0.2709

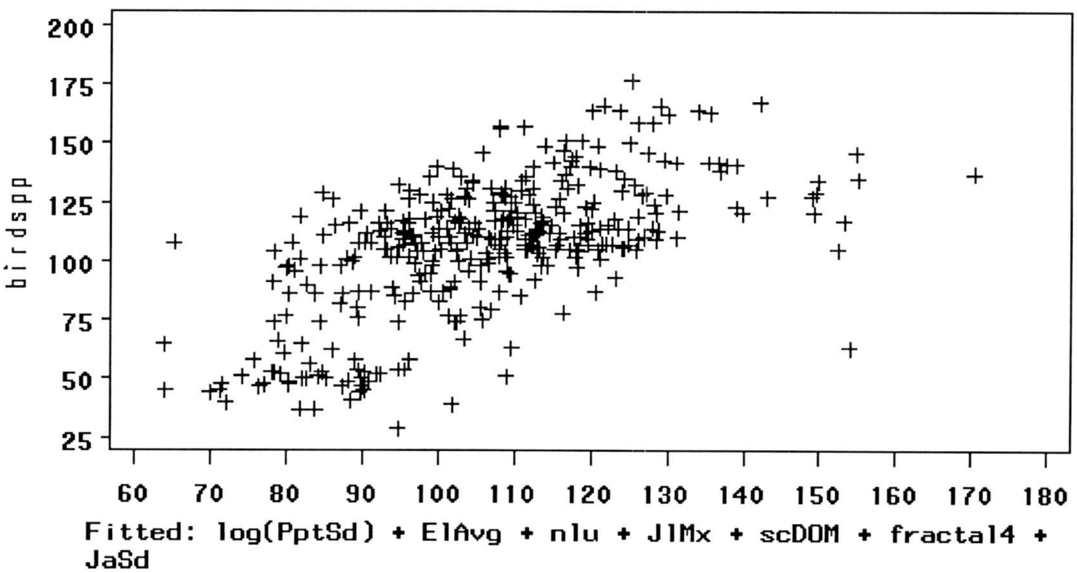
Variables	Regression Coefficient	*t*	*P*
Intercept	4.4986	43.13	<0.0001
JaMn	0.032	10.08	<0.0001
ElAvg	0.0002	7.51	<0.0001
Nlu	0.008	3.97	<0.0001
fractal4	-0.116	-4.3	<0.0001
RvrTot	0.0006	3.26	0.0012
SeasSd	0.081	3.18	0.0016
SeasAvg	0.015	3.26	0.0012

Table 4, Continued

Ecoregion 7.1 – Marine West Coast Forest

Birdspp =

120.72 + 8.2159 lPptSd + 0.0102 ElAvg + 0.3631 nlu – 2.7303 JlMx – 11.849 scDOM – 10.358 fractal4 +
(16.427) (1.567) (0.003) (0.122) (0.538) (3.676) (3.620)
4.6044 JaSd
(1.640)



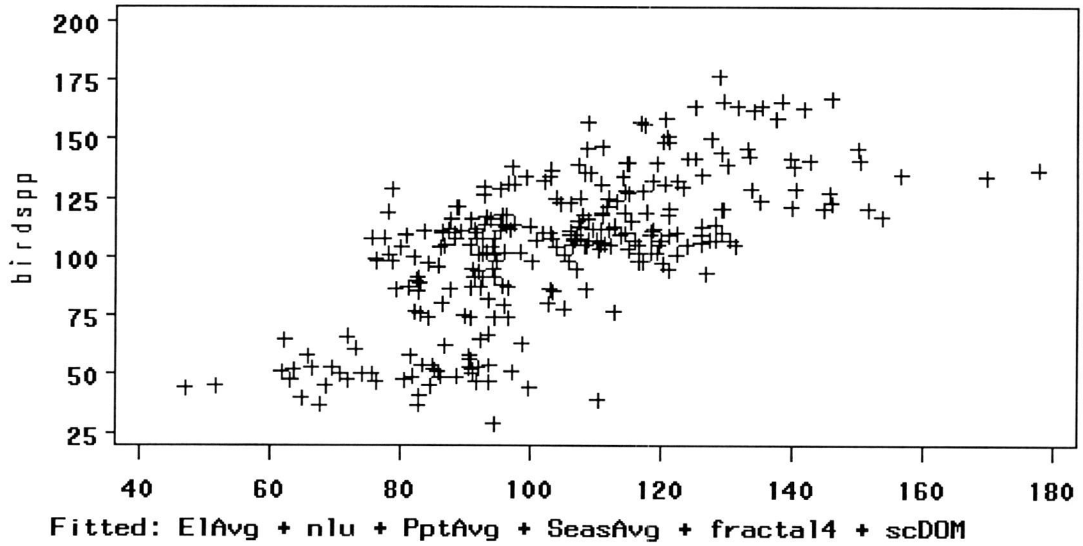
N=370
R square=0.370
Adjusted R^2=0.358
Cp=8.000
RMSE=22.658

Variables	Regression Coefficient	*t*	*P*
Intercept	**120.72**	7.35	<0.0001
log(PptSd)	8.216	5.24	<0.0001
ElAvg	0.01	4.02	<0.0001
nlu	0.363	2.99	0.003
JlMx	-2.73	-5.07	<0.0001
scDOM	-11.849	-3.22	0.0014
fractal4	-10.358	-2.86	0.0045
JaSd	4.604	2.81	0.0053

Table 4, Continued

Ecoregion 10.1 – Western Interior Basins and Ranges

Birdspp =
122.85 + 0.0262 ElAvg + 0.7994 nlu + 0.0539 PptAvg – 2.9935 SeasAvg – 12.986 fractal4 - 10.305 scDOM
(19.428) (0.003) (0.132) (0.011) (0.776) (4.391) (5.019)



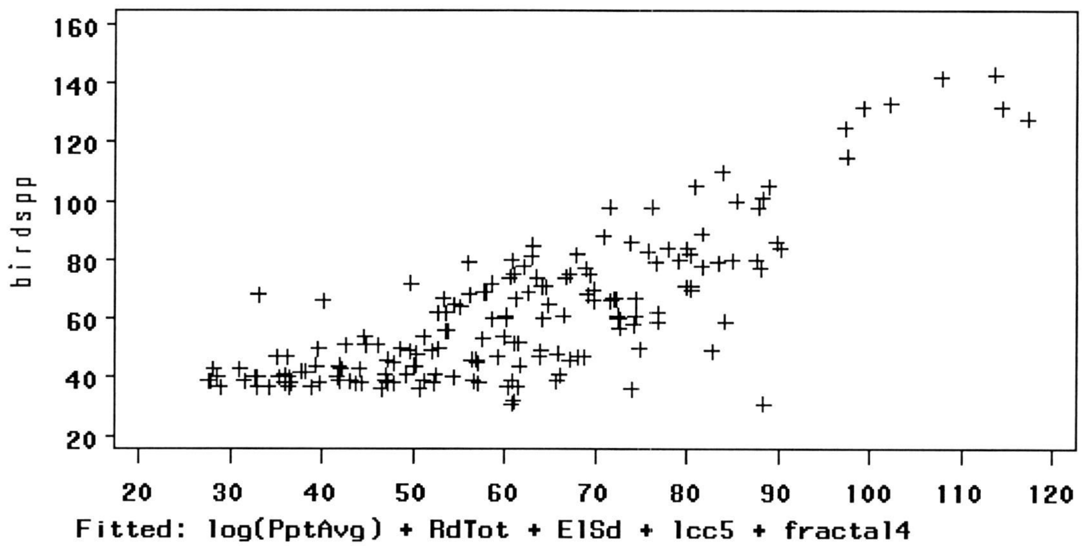
N=284
R square=0.458
Adjusted R^2=0.447
Cp=7.000
RMSE=23.007

Variables	Regression Coefficient	*t*	*P*
Intercept	122.85	6.32	<0.0001
ElAvg	0.026	9.83	<0.0001
nlu	0.799	6.04	<0.0001
PptAvg	0.054	4.99	<0.0001
SeasAvg	-2.993	-3.86	<0.0001
fractal4	-12.986	-2.96	0.0034
scDOM	-10.305	-2.05	0.041

Table 4, Continued

Ecoregion 10.2 – Sonoran and Mohave Deserts

Birdspp = -48.944 + 13.219 lnlu + 17.929 lPptAvg + 0.2416 RdTot +0.0241 ElSd – 12.054 lcc5 – 10.361 fractal4
(16.994) (1.220) (3.277) (0.054) (0.008) (4.320) (4.532)



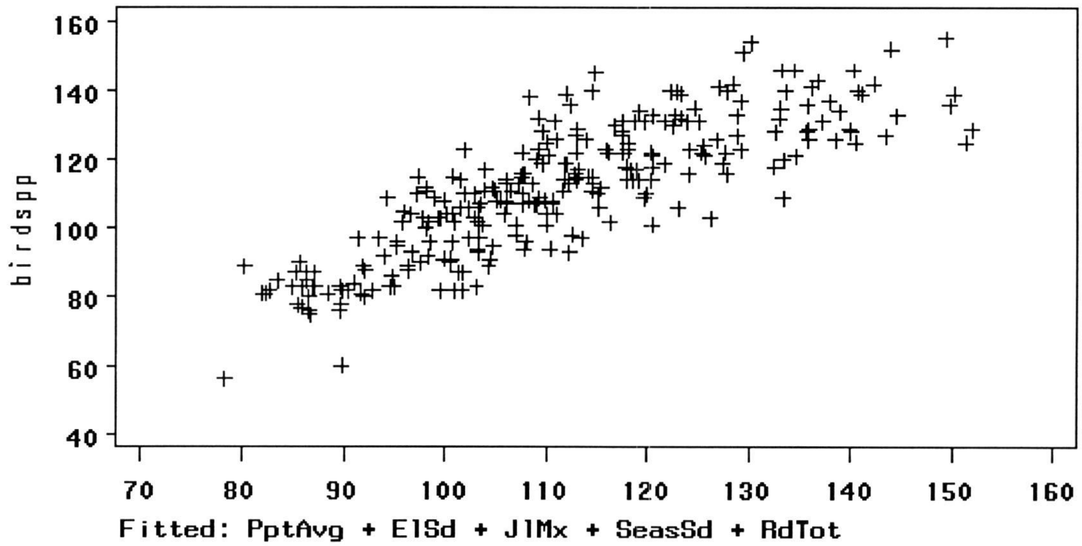
N=175
R square=0.619
Adjusted R^2=0.606
Cp=7.000
RMSE=14.919

Variables	Regression Coefficient	*t*	*P*
Intercept	-48.944	-2.88	0.0045
log(PptAvg)	17.929	5.47	<0.0001
RdTot	0.242	4.46	<0.0001
ElSd	0.024	3.03	0.0029
lcc5	-12.054	-2.79	0.0059
fractal4	-10.361	-2.29	0.0235

Table 4, Continued

Ecoregion 11.1 – Mediterranean California

Birdspp = 112.99 + 0.0421 PptAvg + 0.0721 ElSd – 1.3337 JlMx – 3.9555 SeasSd + 0.044 RdTot
(6.381) (0.003) (0.006) (0.220) (1.435) (0.020)



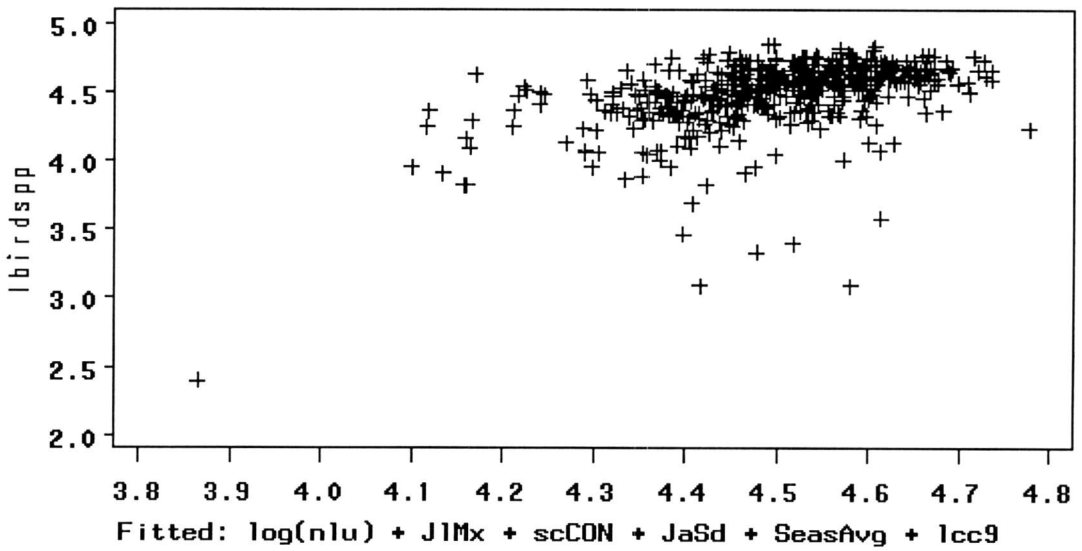
N=264
R square=0.690
Adjusted R^2=0.684
Cp=6.000
RMSE=10.761

Variables	Regression Coefficient	*t*	*P*
Intercept	112.99	17.71	<0.0001
PptAvg	0.042	12.62	<0.0001
ElSd	0.072	12.56	<0.0001
JlMx	-1.334	-6.08	<0.0001
SeasSd	-3.956	-2.76	0.0063
RdTot	0.044	2.16	0.032

Table 5 The following are summary tables of the regression results for the (a) Chesapeake region and (b) its ecoregions. Models are given with regression coefficient standard errors beneath. Also listed are the number of hexagons used in the regression, the R-squared values, adjusted R-squared values, Mallow's Cp statistics, and root mean square errors. The tables illustrate the significance of variables in the model.

(a) Chesapeake Region Model

Lbirdspp= 4.3633 + 0.2439 lnlu - 0.0338 JlMx - 0.5502 scCON + 0.1245 JaSd + 0.0272 SeasAvg + 0.1453 lcc9
(0.368) (0.024) (0.008) (0.110) (0.023) (0.009) (0.044)



N=555
R square=0.228
Adjusted R^2=0.210
Cp=7.000
RMSE=0.2138

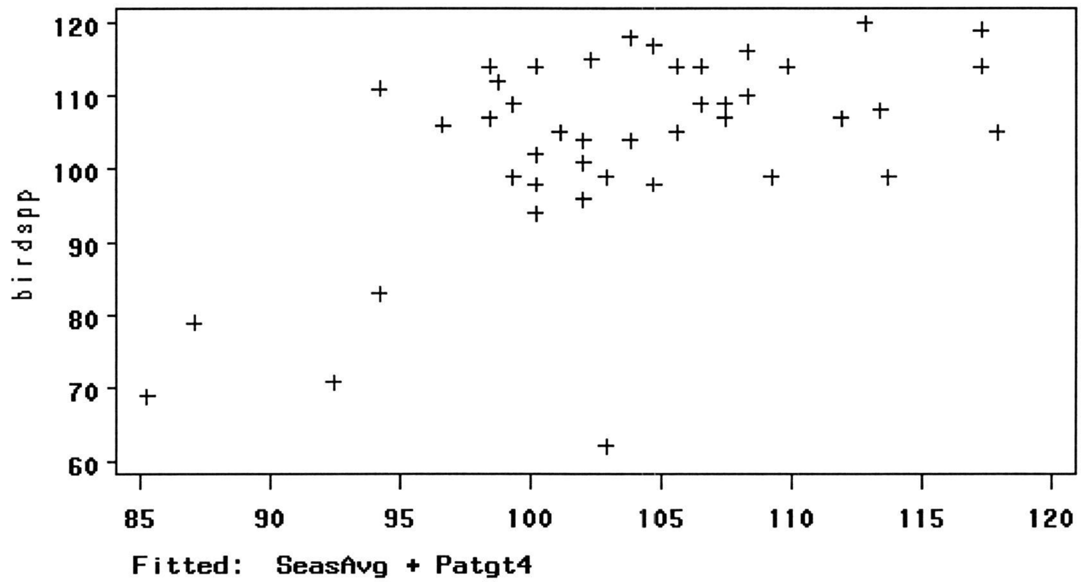
Variables	Regression Coefficient	*t*	*P*
Intercept	4.3633	11.86	<0.0001
log(nlu)	0.244	10.24	<0.0001
JlMx	-0.034	-4.19	<0.0001
scCON	-0.55	-4.99	<0.0001
JaSd	0.125	5.42	<0.0001
SeasAvg	0.027	2.94	0.0034
lcc9	0.145	3.33	0.0009

Table 5, Continued

(b) Chesapeake Ecoregion Models

Ecoregion 5.3 – Atlantic Highlands

Birdspp = 379.164 – 11.393 SeasAvg + 0.8993 patgt4
(92.571) (3.696) (0.300)



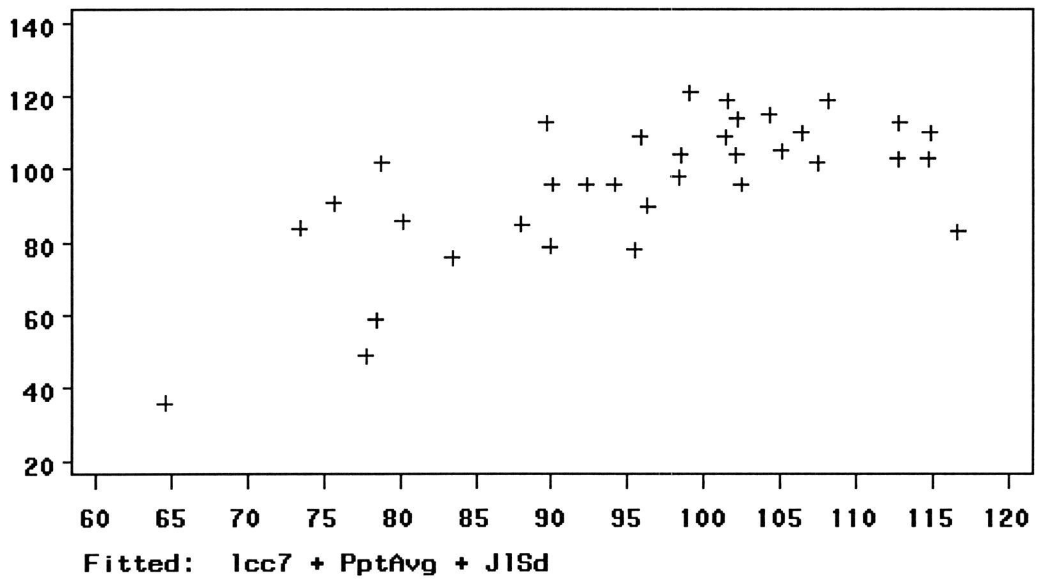
N=43
R square=0.300
Adjusted R^2=0.265
Cp=-2.380
RMSE=11.435

Variables	Regression Coefficient	*t*	*P*
Intercept	379.164	4.10	0.0002
SeasAvg	-11.393	-3.08	0.0037
Patgt4	0.899	2.99	0.0047

Table 5, Continued

Ecoregion 8.1 – Mixed wood Plains

Birdspp = -12.551 + 24.027 lcc7 + 0.0816 PptAvg + 11.593 JlSd
(34.924) (5.631) (0.033) (5.375)



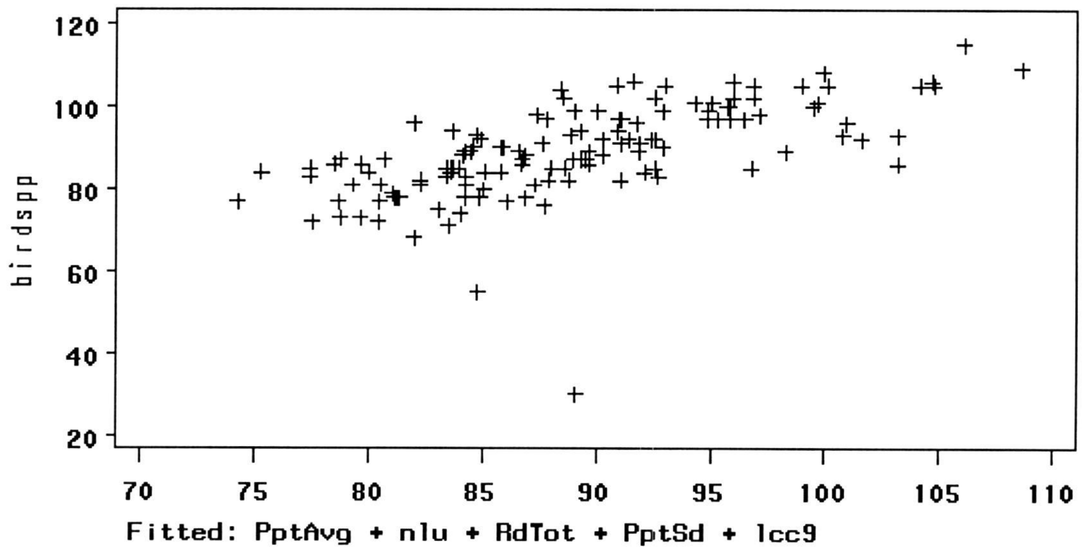
N=35
R square=0.458
Adjusted R^2=0.406
Cp=4.000
RMSE=14.982

Variables	Regression Coefficient	*t*	*P*
Intercept	-12.551	-0.36	0.7217
lcc7	24.027	4.27	0.0002
PptAvg	0.082	2.49	0.0185
JlSd	11.593	2.16	0.0389

Table 5, Continued

Ecoregion 8.3 – Southeastern USA Plains

Birdspp = 198.86 – 0.112 PptAvg + 0.3971 nlu + 0.0566 RdTot + 0.2604 PptSd – 4.0713 lcc9
(22.077) (0.020) (0.149) (0.021) (0.100) (1.966)



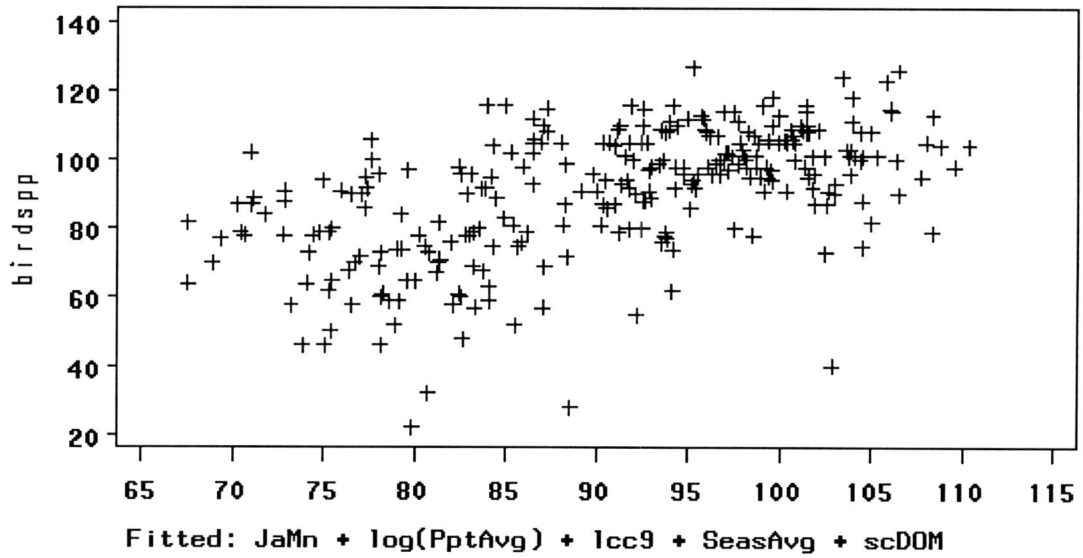
N=131
R square=0.402
Adjusted R^2=0.378
Cp=6.000
RMSE=8.9496

Variables	Regression Coefficient	*t*	*P*
Intercept	198.86	9.01	<0.0001
PptAvg	-0.112	-5.71	<0.0001
nlu	0.397	2.67	0.0085
RdTot	0.057	2.68	0.0084
PptSd	0.26	2.6	0.0103
lcc9	-4.071	-2.07	0.0404

Table 5, Continued

Ecoregion 8.4 – Ozark, Ouachita-Appalachian Forests

Birdspp = 220.92 – 3.7018 JaMn – 32.121 lPptAvg + 16.07 lcc9 + 3.2033 SeasAvg – 4.4764 scDOM
(88.171) (0.485) (11.389) (4.302) (0.846) (2.183)



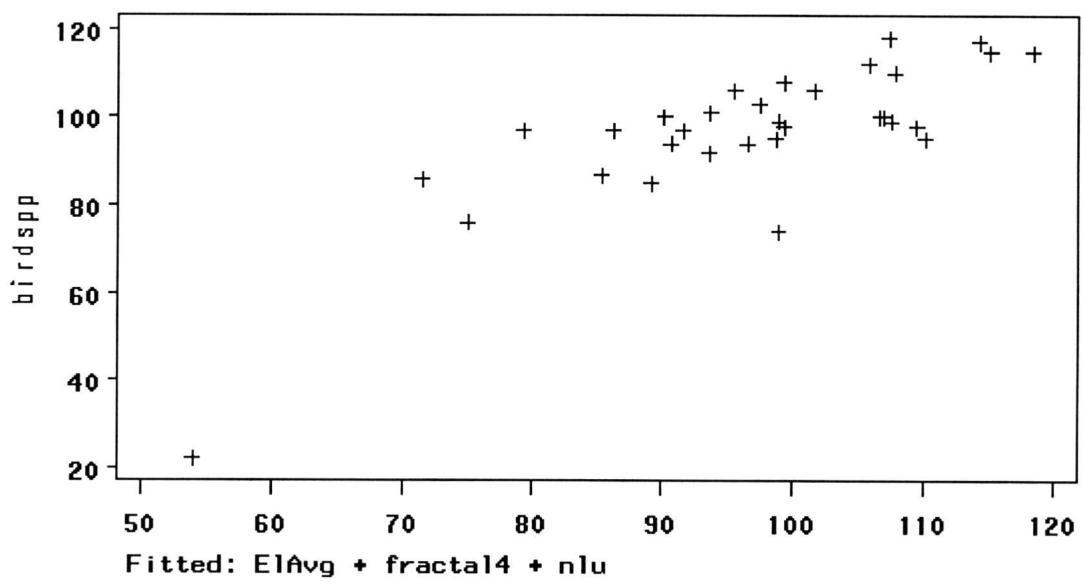
N=279
R square=0.306
Adjusted R^2=0.293
Cp=6.000
RMSE=15.612

Variables	Regression Coefficient	*t*	*P*
Intercept	220.92	2.51	0.0128
JaMn	-3.702	-7.62	<0.0001
log(PptAvg)	-32.121	-2.82	0.0051
lcc9	16.07	3.74	0.0002
SeasAvg	3.203	3.79	0.0002
scDOM	-4.476	-2.05	0.0413

Table 5, Continued

Ecoregion 8.5 – Mississippi Alluvial and Southeast USA Coastal Plains

Birdspp = 73.188 – 1.6076 ElAvg + 14.522 fractal4 + 0.7291 nlu
(11.9541) (0.325) (4.299) (0.299)



N=32
R square=0.628
Adjusted R^2=0.589
Cp=4.000
RMSE=11.098

Variables	Regression Coefficient	*t*	*P*
Intercept	73.188	-4.94	<0.0001
ElAvg	-1.608	-4.94	<0.0001
fractal4	14.522	3.38	0.0022
nlu	0.729	2.44	0.0215

West Coast Region

The West Coast region, made up of 1,437 hexagons, covers California, Oregon, and Washington. A great portion of the region is bordered by the Pacific Ocean, greatly affecting the climate and vegetation. Coastal mountain ranges, interior mountain ranges, and valleys create a diversity of habitat types and land use classes. The model developed for the West Coast region explains 62.5% of the variation in bird species richness that occurs over the area (see Table 4).

Ten of the variables included in this final model were measures of the proportion of area in different land use classes. These land cover classes included cropland/pasture mixtures, grassland/cropland mixtures, grass dominated, shrub dominated rangeland, grass/shrub rangeland mixtures, conifer forests, water bodies, barren/sparsely vegetated, alpine tundra, and urban. All variables had a positive relationship with bird species richness with the exception of alpine tundra. Any proportion of land in the hexagon characterized by the alpine tundra class reduces bird species richness. Proportion of the hexagons characterized by water bodies positively affects bird species richness. A suggested reason being that at such large spatial scales, water bodies tend not to be a common habitat type. Water bodies might present a unique set of bird species, thus increasing the total richness (Bohning-Gaese 1997). The total kilometers in streams, positively correlated with richness, is another indication of the importance of water bodies and riparian habitat.

Also demonstrating to be influential in predicting the number of bird species are climatic conditions. In terms of temperature, explanatory variables such as January temperature standard deviation, seasonal average, and seasonal standard deviation were negatively correlated with bird species richness. A positive relationship was indicated with precipitation standard deviation. These are all indicative of climatic processes, which in turn can be related to the productivity.

Several other explanatory variables appeared in the model. The average elevation measure within the hexagons has a positive correlation with bird species richness. The positive relationship that average elevation has with bird species richness does not follow the hypothesis as stated by Ricklefs and Schluter (1993). They suggest that species richness decreases with increasing elevation. In this region, however, elevations may not reach extremes where climate and vegetation are not conducive to high species richness.

West Coast Ecoregions

For the West coast and Chesapeake regions both, there ended up being 5 groupings of the hexagons according to the level II ecoregion delineations. For the West coast region, the greatest number of hexagons in an ecoregion was 495 and the smallest number of hexagons in a grouping was 175 (Table 4). Appearing in all models for ecoregions of the West coast was some measure of elevation, the average or standard deviation, indicating topography as a process influencing bird species richness in all the West coast ecoregions. Its relationship with bird species richness was always positive. Landscape metrics and climatic variables also play a significant role in determining bird species richness in all models.

The Western Cordillera Ecoregion consists of the northern portion of California stretching down along the eastern side of the Sierra Nevada mountain range. It also consists of the Cascade ranges in Oregon and Washington, and the northeastern portion of both these states. There is a range of elevations within this ecoregion. Characteristic of this ecoregion is mixed forests, coniferous forests, to alpine meadows. Northern portions of this ecoregion tend to be more humid with increased precipitation. High elevations in the mountain ranges receive snow. And, the eastern portions of the mountain ranges tend to be drier (CEC, 1997).

The model developed for this ecoregion explains 23.3% of the variation in bird species richness. Significant variables in the models include several temperature variables all having a positive relationship with bird species richness. These are seasonal averages, seasonal standard deviations, and January minimum temperatures. Average elevation also plays a significant role in determining richness. An increase in average elevation results in higher richness. Several landscape metrics also were significant in the model. One determinant of richness is the fractal metric. This is a measure of how much patches of similar land cover classes vary within one hexagon. Greater values of this measure indicate more variability in patches, and thus more negatively influence bird species richness. The number of land use classes positively influences richness. Also, the total river kilometers variable is significant in the model with a positive correlation of richness with this indicator of riparian habitat.

The Marine West Coast Ecoregion consists of the northern coast of California, and the coastal areas of Oregon and Washington. Typical of this ecoregion is moist, temperate climates with dense conifer forests. Elevations range from sea level to above 5,000 feet. This model explains 37.0% of the variation in species richness. Again, landscape metrics are significant determinants in this model. Both the dominance metric and fractal metric have a negative relationship with species richness. The dominance metric is a measure of how much one type of land cover class dominates within a hexagon. In this model, the more one land cover class dominates the more negatively it influences bird species richness. In terms of climatic variables, precipitation standard deviation has a positive relationship with species richness. July maximum temperatures have a negative relationship with species richness. January standard deviations have a positive relationship.

The Western Interior Basin and Range Ecoregion consists of the southeast and central portions of both Oregon and Washington. This area was made up of 284 hexagons. Climate of this ecoregion tends to be semiarid and cool. The dominant vegetation is that of sagebrush steppe habitat. Elevations range from low elevation hills to plains at elevations of 6,000 – 8,000 feet. The model developed explained 45.8% of the variation in species richness. One significant determinant in this model is average elevation. Higher elevations correlate positively with higher bird species richness. Two climatic variables appeared in the model. Seasonal average has a negative correlation, whereas average precipitation has a positive relationship with richness. Three landscape metric variables are included in this model. They are the fractal metric and dominance metric, both having a negative relationship with bird species richness, and number of land use classes with a positive relationship.

The Sonoran-Mohave Deserts Ecoregion consists of the southeastern portion of California. It was made up of 175 hexagons. Climate in this ecoregion is moderate in the winters, long, hot summers, and low levels of precipitation. The vegetation is usually sparse. Elevations can range from below sea level to 11,000 feet. The topography is made up of valleys, basins, and dry, rocky mountain ranges. This model explains 61.9% of the variation in bird species richness within the ecoregion. The average precipitation variable is one significant determinant in the model. It is not surprising that in such a dry ecoregion bird species richness would have a positive relationship with average precipitation. The standard deviation in elevation also has a positive relationship with richness. Total roads in this area may be an indication of disturbance process positively influencing richness. Another determinant of richness is the proportion of area of each hexagon in shrub-dominated rangeland. This land cover class had a negative relationship with bird species richness. The fractal metric having a negative relationship indicates larger patches of habitat are negatively correlated with richness.

The Mediterranean California Ecoregion consists of the southern coastal and central portions of California. This ecoregion is made up of 264 hexagons. Typical climate is mild winters and hot summers with precipitation mostly in the winter months and often a shortage during the summer months. Vegetation consists of evergreen shrubs and trees, grasslands, extensive agriculture, sagebrush, and riparian forests. The model explains 69.0% of the variation in bird species richness in these hexagons. Average precipitation has a positive correlation with richness. Seasonal standard deviation and July maximum temperatures have negative relationships with richness. Elevation standard deviation has a positive correlation with richness. The total roads variable is also positively correlated with richness. In drier, hotter climates typical of this ecoregion, higher bird species richness is more dependent on rainfall areas, and those areas with fewer extremes in the temperature.

Chesapeake Region

The Chesapeake region covers a much smaller area with less than half the number of hexagons (n = 555) than the West coast region (n = 1,437). The greatest portion of the Chesapeake region is in Southeastern plains, the Appalachian Mountains, and the Appalachian plateaus. A very small portion is in coastal plains, bordered to the east by the Atlantic Ocean. Precipitation tends to be evenly distributed throughout the year, with some periods of heavier precipitation. Vegetation varies somewhat with topography and elevation, but generally is characterized by broadleaf deciduous and temperate evergreen.

The model developed for the Chesapeake region explains 22.8% of the variation in bird species richness of this region (Table 5). Of all the variables that were attempted in the model, six variables were significant in determining the richness distributions for this region. The model indicates that the number of land use classes positively influences richness across the region. However, less heterogeneity of land use classes will have a negative impact on richness as indicated by the contagion metric. In terms of climate, July temperature maximum will negatively influence number of species, but seasonality will have a positive influence. And, as expected of this region, areas of mixed, conifer and deciduous, forests will positively affect richness.

Some similarities in the region model and ecoregion model did occur. Similar to the mixed forest variable in the region model, three ecoregion models had either the variable indicating the proportion of area in deciduous forest or in deciduous/conifer forest. These variables have a positive relationship on richness in the Mixed Wood Plains, Ozark, Ouachita-Appalachian Forests ecoregions as well, but the Southeastern USA Plains ecoregion has a negative influence on richness. This negative influence perhaps is due to another habitat type being even more supportive of greater richness. The mixed forest variable still was significant enough to enter the model, but with a negative influence.

With the ecoregion groupings made in this study we see that smaller areas within this region have other determinants that are significant. No variables related to precipitation appear in the Chesapeake region model. However, the annual average precipitation variable is significant in three of the five ecoregion models. Overall, there is abundant precipitation in this region. As expected, this wouldn't be a significant determinant of richness for this region. But, by grouping the hexagons by ecoregion we see that it does become a significant determinant in particular areas of this region. These areas include the Mixed Wood Plains, Southeastern USA Plains, and the Ozark, Ouachita-Appalachian Forests.

Chesapeake ecoregion models

Each ecoregion model developed tells its unique story of how the species richness distributions are made. Only 43 hexagons of the northern portion of this region fall within the Atlantic Highlands ecoregion. The Atlantic Highlands Ecoregion consists of a very small portion of north-central Pennsylvania and a small portion on eastern side of Pennsylvania. The model developed explains 30.0% of the variability in bird species richness. Characteristic of this ecoregion are higher elevations, more continental climates, and abundant precipitation, also in the form of snow. Unlike the region as a whole, the seasonality here has a negative influence on species richness. One landscape metric was also significant. The number of larger patches (of size greater than 4 pixels) positively influences richness. This can be interpreted as the greater the patch size, and fewer disturbances, the greater the species richness.

The Mixed Woodland Plains Ecoregion consists of small portion of northwest Pennsylvania, and another small portion in northeast Pennsylvania. This model explains 45.8% of the variation in species richness. The number of hexagons in this ecoregion is 35. The topography of this ecoregion is diverse. Glacier carved mountains and sedimentary plateaus also result in diverse vegetation. But, the dominant vegetation is described as temperate deciduous. One significant variable in the model is the proportion of land in deciduous forest with a positive influence on richness. The climate is described as continental with cold winters, warm summers, and year-round precipitation. In terms of climate, both average precipitation and July temperature standard deviation are positively correlated with species richness.

The Southeastern Plains Ecoregion consists of eastern portion of Virginia, the northeast portion of Maryland, and southeastern Pennsylvania. This model explains 40.2% of the variation in bird species richness. The number of hexagons included in this ecoregion is 131. Characteristic of this ecoregion is lower elevations, abundance of wet habitat, mild winters, hot and humid summers, and precipitation evenly distributed throughout the year. Average precipitation has a negative influence on bird species richness in this ecoregion. However, the standard deviation in precipitation has a positive correlation with richness. Both the number of land use classes and total roads has a positive correlation with richness indicating heterogeneity and disturbance increase richness. The variable measuring area in deciduous/conifer forest has a negative influence on richness. The reason for this land cover class having a negative relationship is perhaps because of the presence of numerous water bodies and moist habitat types which support a greater number of bird species.

The Ozark, Ouachita-Appalachian Forests Ecoregion consists of central portion of Pennsylvania, the entire state of West Virginia, and the western part of Virginia. This model explains 30.6% of the variation. The ecoregion is made up of 279 hexagons. This ecoregion consists of low mountains and valleys. The dominant vegetation is mixed oak-pine forest. And, the climate is temperate with distinct summers and winters. January minimum temperatures and average precipitation negatively influence richness, whereas seasonality is positively correlated. The amount of area in deciduous/conifer forests has a positive relationship with richness. The measure of how much one land use class dominates negatively influences richness, an indication of the importance of heterogeneity in this ecoregion.

The Mississippi Alluvial/Coastal Plains Ecoregion consists of the whole of Delaware, southern Maryland, and eastern portion of Virginia. This model explains 62.8% of the variation. The ecoregion is made up of 32 hexagons. Characteristic of this ecoregion are low elevations, coastal plains and marshes, interior swamps, low seasonality, and abundant precipitation. Climate seems to be less influential to richness in this ecoregion because of the fact that this is a mild, moist climate. Other variables, such as elevation, number of land use classes, and elevation, become significant to richness. Elevation is negatively correlated with richness indicating that richness is higher at lower elevations such as the coastal plains. The fractal metric has a positive relationship with richness. Greater number of land use classes also is correlated with higher richness.

Concluding remarks

Biodiversity has many definitions. As Noss (1990) suggests, one way of circumventing this is to approach issues in biodiversity with measurable indicators. Using species richness as the measured indicator, this study investigated one issue concerning biodiversity. This issue involves the question of what determines bird species richness distributions. One goal of this study was to determine measurable variables that predict patterns of bird species richness. Another goal was to look at and compare significant variables at two levels of grouping.

The measurable variables determined to be significant in predicting richness are also representative of processes. Significant variables in the two models at the region level of grouping indicate that processes such as climate, productivity/available energy, and habitat heterogeneity are important in determining bird species richness distributions. This supports several hypotheses developed in past, large-scale studies (Flather et al. 1992, O'Connor et al. 1996, etc.) depicted in Table 1. For example, Currie's study (1991) hypothesized that species richness increases with productivity and available energy.

Differences in predictors for the two regions result because of differences in location and landscape patterns. The climate and topography vary between the two regions because of location. Precipitation patterns, temperatures, seasonal variations, elevation, etc. are going to differ resulting in unique vegetation patterns, in turn resulting in different number of species. As well, different species will respond differently to these patterns. The use of this vegetation by humans, and the amount of patchiness, and the types of land use classes will also influence to species richness distributions.

What was hypothesized prior to this study was that ecoregional differences would result in different processes determining bird species richness. Variation within the two regions discussed did result in models that differ. But, similar processes seem to working at both levels of grouping. The most common processes evident within each of the ecoregions are climate, topography, habitat heterogeneity, and productivity/available energy. Disturbance was evident in some of the ecoregions.

The uniqueness of the ecoregion, and the influence it has on the bird species richness distributions, becomes evident in the models. These slight variations within the regions, whether it is due to topography, land use, vegetation, etc., help to identify areas that are classified into these ecoregions. Evident also in the models, these slight variations are those that create differences in richness.

The models developed for each of the ecoregions, and the interpretations of these models further reinforce the idea of connectivity of ecosystems and bird species. What processes are shaping the ecosystem are in turn shaping the distributions of bird species. In terms of management implications and conservation of species richness, maintaining ecosystems, and the processes functioning on these ecosystems, are pertinent to maintaining bird richness. Also, maintaining habitat heterogeneity and particular types of land cover classes (maybe those of significant productivity) is also necessary for high richness.

Proposed further research

There are limitations with this dataset. With limitations in the dataset presents opportunities for improvements and further research. One such limitation is the size of the hexagons. The explanatory variables used in this study describe conditions averaged over 640 square kilometers. Generalizing such variables as average precipitation over the area of the hexagon presents a problem with the accuracy and precision of explaining the distributions and numbers of species. The true explanations may be masked by the over-generalizations. However, the study does serve the purpose of coarse scale bird species distribution study. A possible next step would be to subdivide the hexagons into smaller polygons.

The geographic area over which the data was collected not only is limited, but the also uses state lines as boundaries. These boundaries have no ecological significance and affect results due to discontinuity. A suggestion would be to expand the dataset to include the conterminous US, and to divide up into larger geographic regions. Another suggestion would be to collect data for entire ecoregions, and develop models for these. In this study only data for portions of ecoregions was analyzed. Suggested methodology for continuing this study is to use classification and regression tree analysis. The purpose of using this method would be to develop a map of spatial patterning of bird species richness across the geographic regions. This map would reflect subsets of bird species richness divided according to their responses to the explanatory variables (Breiman et al. 1994).

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