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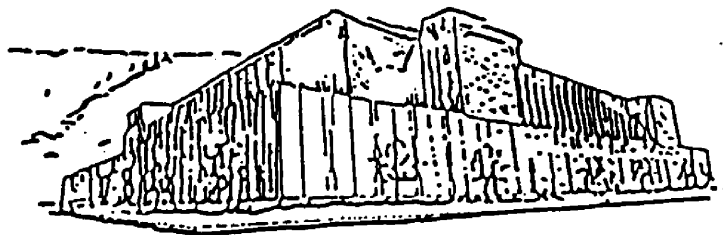
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*On the Relationship Between Avian Species Richness  
and Net Primary Productivity  
in Western Montana*

by

Polly C. Thornton

B.S. Colorado State University

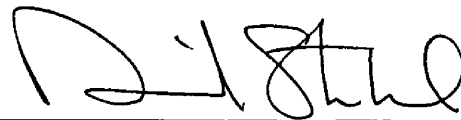
presented in partial fulfillment of the requirements  
for the degree of  
Master of Science

The University of Montana  
Wildlife Biology Program  
1997

Approved by:



Committee Chair



Dean, Graduate School

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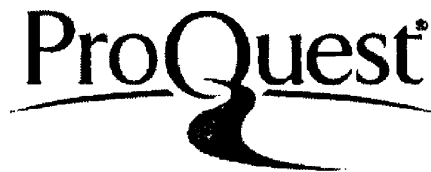


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On the Relationship Between Avian Species Richness and Net Primary Productivity in Western Montana

Advisor: Roland Redmond



The goal of this study was to estimate net primary production at a landscape scale and then to examine its relationship with avian species richness as measured by field surveys. Net primary production was estimated with an ecosystem process model, FOREST-BGC. In contrast to an number of previous field studies, no relationship was found between net primary productivity and avian species richness. Graphical analysis revealed large amounts of scatter, correlation coefficients were low, and productivity was not retained as a significant variable in multiple regression analysis. Strong correlations were found, however, between avian species richness and vegetative structural variables. Discrepancies between this and previous studies of the productivity-species richness relationship are may be due to differences in methods for estimating net primary productivity, and the scale at which the relationship was examined.

## *Acknowledgments*

I have benefited from the guidance and support of many people throughout this endeavor, for which I am most grateful. In particular, I whole-heartedly thank my brother, Peter Thornton, for his help in more ways than I have space here to enumerate. I also thank Melissa Hart, the arch-mage of ARC, for helping me to learn ARC/INFO and answering syntax question after syntax question! I have learned an enormous amount about GIS technology from several people at the Wildlife Spatial Analysis Lab. Thank you all. I also owe great thanks to the Boone and Crockett Club, Dr. Hal Salwasser, and Dr. Dan Pletcher for support in the initial phase of this project. I would not have been able to conduct this study without the support of both Dr. Steve Running and Dr. Richard Hutto. I thank Dr. Hutto for allowing me to use his avian census data, and Dr. Running for allowing me to use his ecosystem process models and computing capacity, for letting me tap into the knowledge of the Numerical Terradynamic Simulation group, and for three months of rope. I am very grateful to my advisor, Dr. Roland Redmond, for accepting me as a graduate student and taking me into the Wildlife Spatial Analysis Lab, and for reading so many versions of my thesis and helping me make sense of it all; thank you very much.

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## **1. Introduction**

Biological diversity, according to one familiar definition, is the variety and variability of living organisms and the ecological complexes in which they occur (OTA, 1987). This variety of life, how it came to be, the role it plays in sustaining ecosystems, and the influence we humans have on it, has been of interest since at least the time of Charles Darwin. Whether it is out of concern for the intrinsic value of all organisms, the potential to improve human society, or an interest in maintaining the integrity of ecosystems, the maintenance of biological diversity is of growing public, national, and international concern (Nash 1989, National Research Council 1989b, National Science Board 1989, McNeely et al., 1990). Accordingly, in the scientific arena, a primary focus in community ecology has been the determination of how biotic and abiotic factors interact to produce patterns of biological diversity (Brown 1981, Connell and Orias 1964, Currie 1991, Diamond 1988, Fischer 1960, Huston 1994, Hutchinson 1959, MacArthur 1964, Owen 1990, Parrish and Salia 190, Pianka 1967, Simpson 1964) Understanding the regulation of diversity is essential for guiding habitat preservation, ecosystem restoration, and conservation strategies (Lubchenco, et al. 1991, Marañon and Garcia 1997).

This rich history has produced a wealth of theories describing the factors that regulate biological diversity. The six most prominent of these theories are described here in brief. 1) Greater diversity may develop in regions that have existed in their current state for longer periods of time because there has been the time needed for speciation. (Devey 1949, Elton 1958, Newell 1962, Simpson 1964). 2) Regions with greater structural heterogeneity could support greater diversity by allowing for more functional

structural heterogeneity could support greater diversity by allowing for more functional types of species, each exploiting either different resources, or the same resources in different ways (Miller 1958, MacArthur 1964, Simpson 1964). 3) Competition may increase diversity by forcing species to be more specialized, provided no one species has so great a competitive advantage as to drive other species to extinction (Dobzhansky 1950, Williams 1964). 4) A nearly opposite mechanism is that predation lowers prey populations enough to reduce competition, which thereby permits the co-existence of additional prey species, which support additional predators (Paine 1966, Parrish and Salia 1970). 5) Regions with stable climates may have a constant supply of resources, allowing species to specialize, and increasing diversity through smaller niches (Klopfer 1959). 6) Finally, regions with greater productivity have more energy, to be divided into more pieces, and therefore greater diversity is possible (Brown 1981, Connell and Orias 1964, Hutchinson 1959). There is no single theory that explains all observed patterns of diversity, and diversity is likely influenced by several factors (Diamond 1988, Huston 1994, Pianka 1966). The relative importance of each factor may vary according to what taxonomic group is being studied, where, and at what scale (Huston 1994, Ricklefs 1987).

Mapping and monitoring biological diversity using remotely sensed data is gaining increasing support (Lubchenco, et al. 1991, Scott, et al. 1990, Soulé and Kohm 1989, Stoms and Estes 1993). Large portions of the planet are not easily accessible by ground, and it is not feasible to conduct surveys of these areas even once, let alone on a

periodic basis. An advantage of remote sensing techniques is that satellite sensors can cover large areas repeatedly. These sensors can detect vegetation properties, such as greenness and biomass, but they cannot detect the number of species, or the population sizes of most organisms. To bring remote sensing techniques into the study of diversity, it is necessary to determine if there are relationships between environmental properties measurable through remote sensing and biological diversity. If indeed there are such relationships, we can begin to assemble data sets, or compile existing data, to monitor changes in those environmental variables over time. Understanding how the diversity of an area is related to those environmental variables, and how those variables are changing, would allow for periodic monitoring of biological diversity over large geographic areas. Stoms and Estes (1993) suggested net primary productivity as a candidate variable, because it can be quantified by a combination of remote sensing and ecological modeling, and it has been the focus of a great deal of diversity research.

The original theory relating productivity to diversity states that higher productivity yields greater diversity (Preston 1962). This is because scarce species in the most productive regions would be more abundant than scarce species in less productive regions, and would therefore be more resistant to extinction. In a region of high productivity, the available energy can be divided into more pieces before the smallest piece is too small to support the existence of another species. This reasoning has been both supported and contradicted by field studies relating diversity to productivity. A unimodal relationship, in which diversity increases with increasing productivity, but then

decreases as productivity continues to increase, has also been observed ( e.g. Abramsky and Rosenzweig 1984, Tilman 1987). The upslope phase of this relationship, where diversity is increasing with increasing productivity, follows the original theory, and the decline in diversity as productivity continues to increase has been attributed to a variety of mechanisms. These include reduced environmental heterogeneity, reduced dynamic stability, increased predation, and reduced interference competition, with increased productivity (Brown 1971, Brown and Davidson 1977, Rosenzweig 1971, 1972, Tilman 1982, 1987). There are predictions generated by each of these theories that are not always observed, and there is still much disagreement as to the relationship between productivity and diversity (Ricklefs and Schulter 1993, Rosenzweig 1992). It is my goal in this study to explore the relationship between net primary productivity and diversity, to determine if it is possible to map diversity from estimates of net primary productivity derived from remotely sensed data and ecological models. .

Testing for a relationship between productivity and diversity requires a measure of diversity. There is a wide variety of diversity indices in the literature, ranging from a count of the total number of species found, or species richness, to more complex indices that weight the relative abundance of each species. Species richness has been widely used as an index of diversity and is considered to be a suitable measure for most broad-scale comparisons of diversity (Ricklefs and Schulter 1993, Whittaker 1972). Surveying populations of every species, even all vertebrates, is not feasible, and reliable indicators must be chosen to represent the system under consideration (Noss 1990). Songbirds have

been suggested to be efficient indicators because there are many avian species in relation to other vertebrates, they occupy a wide variety of habitat types, and because these species advertise their presence and identity through vocalizations, a large number of species can be monitored with each sampling effort (Hutto 1997). Surveying songbirds, therefore, allows for quantification of diversity using species richness as an index. In this study, I used remote sensing, ecosystem modeling, and field measurements, to determine if there is a relationship between avian species richness and net primary productivity, in hope of establishing a method for incorporating remote sensing techniques into the mapping and monitoring of diversity.

## **2. Study Area**

My study area is bounded by one full Landsat Thematic Mapper (TM) scene (Path41, Row27), covering approximately 32,000 km<sup>2</sup> in western Montana (Fig. 1). Portions of the Missoula valley, Flathead Lake and the Mission mountain range lie within the study area. Valley bottoms are typically grassland with alder, willow, and cottonwood riparian areas. Montane forest types include ponderosa pine (Pinus ponderosa), lodgepole pine (Pinus contorta), western larch (Larix occidentalis), Douglas-fir (Pseudotsuga menziesii), subalpine fir (Abies lasiocarpa) and mixed forest types. High elevation areas are predominantly exposed rock with some alpine tundra.



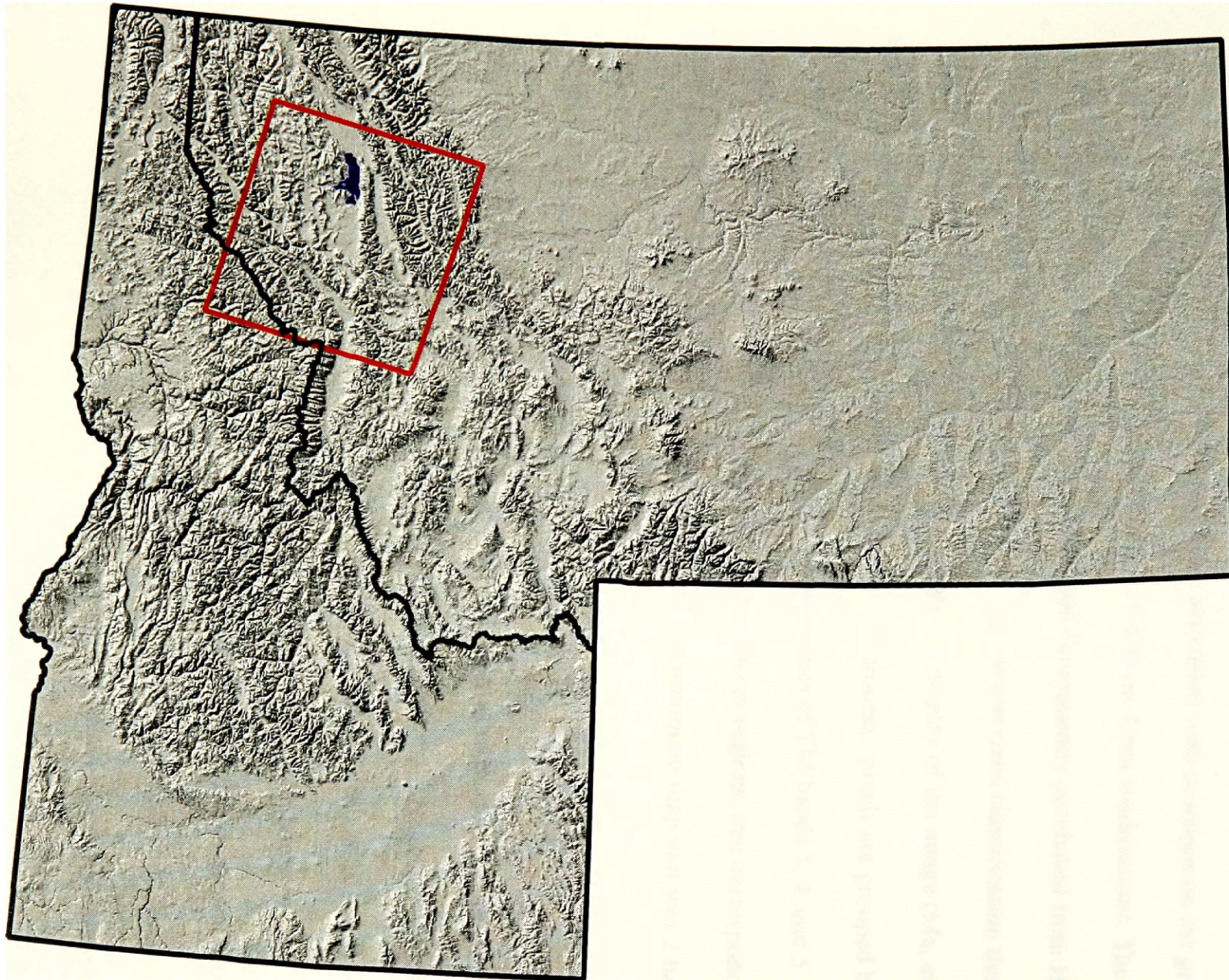


Figure 1. Location of TM scene P41/R27.



### **3. Methods**

Data used in this study came from field and remote sensing sources; all were registered to the Landsat TM scene P41/R27, creating a geographical information system (GIS) database in which multiple variables were associated with positions on the ground. Spatial analysis was done using ARC/INFO (ver. 7.0.4) on Unix workstations. The satellite imagery was acquired on 20 July 1991, and subsequently purchased from Hughes STX corporation by The University of Montana. An unsupervised classification that replicates the patterns visible in a false-color composite display of the image (Ma, et al., unpublished manuscript) was performed. In a two step process, pixels are grouped based on the Euclidean distance of the spectral reflectance values of TM bands 3, 4, and 5. The results of this process are raster polygons, here referred to as regions, that correspond with areas of similar vegetation type on the ground. The minimum map unit was 2 ha.

#### *3.1. Avian Species Richness and Habitat Description*

Avian census data and descriptions of the vegetation at each avian census location were provided by Dr. Richard Hutto at The University of Montana. Transects consisting of 10 point count locations each were established throughout Montana and Idaho, with a total of 3050 points falling in my study area (Fig. 2). Because these locations are distributed across the landscape in groups of 10 multiple points along a single transect fell within the same vegetation type. Individual points were nevertheless considered to be independent samples because each vegetation type was represented by multiple transects

(Hutto 1997). These data, which are part of a long-term study on avian habitat relationships northwestern Montana (Hutto and Hoffland 1996), are a compilation of point-count data from 1992 through 1994. Habitat variables, defined in Table 1, were measured at each point count location, and vegetation types were classified in the field according to the descriptions in Table 2. Point count locations were mapped onto the Landsat satellite scene, and the species richness and vegetation characteristics at each point were entered into the GIS database.

Table 1. Description of vegetation characteristics measured in the field.

Variable	Description
Ground Cover	Percent of ground covered by herbaceous vegetation
Shrub Cover	Percent of ground covered by shrubs > 1m
Bush Cover	Percent of ground covered by shrubs < 1m
Height to Canopy	Height in meters from ground to top of the tree canopy

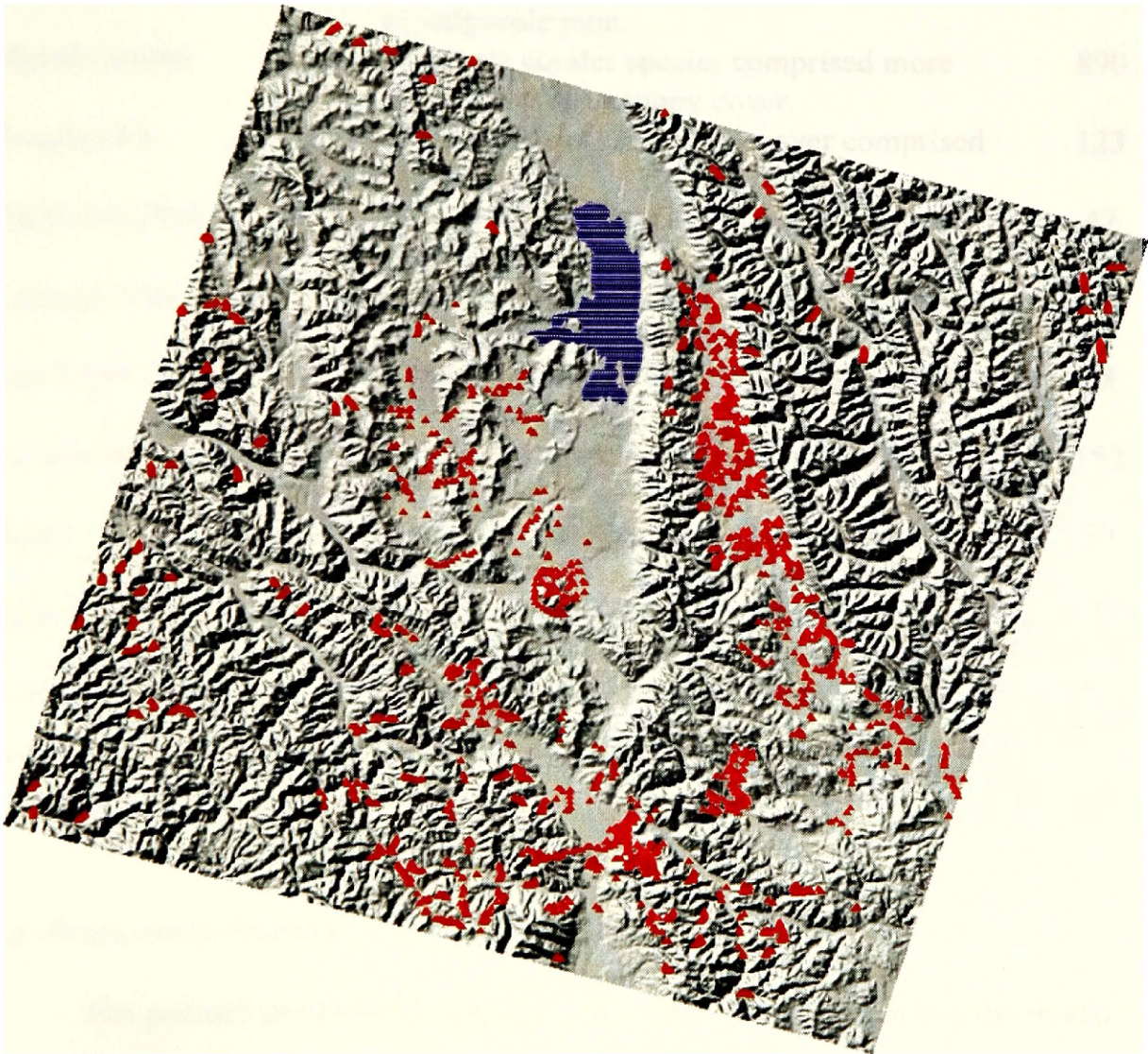


Figure 2. Locations of avian census points.

Table 2. Description of vegetation types, with sample size. Adapted from Hutto and Hoffland, 1996.

Vegetation Type	Description	N
Cedar/Hemlock	At least 80% of the canopy cover comprised of cedar, hemlock or grand fir.	18
Spruce/fir	At least 80% of the canopy cover comprised of spruce, fir, whitebark, or limber pine.	47
Lodgepole Pine	At least 80% of the canopy cover composed of lodgepole pine.	90
Mixed Conifer	No single conifer species comprised more than 80% of the canopy cover.	890
Douglas-Fir	At least 80% of the canopy cover comprised of Douglas fir.	123
Ponderosa Pine	At least 80% of the canopy cover composed of ponderosa pine.	47
Cutting Units	Includes group selection, shelterwood, seed tree, clear-cut and post-fire stands.	681
Sagebrush	Dominated by sagebrush, with some grass and juniper cover.	38
Grassland	Short and mid-grass prairie, grazed and ungrazed.	152
Marsh	Areas with standing water, and either short-saturated marsh, meadow, or willow flats.	52
Riparian Shrub	Well-developed, narrow riparian shrub along relatively fast-flowing streams.	117
Cottonwood/Aspen	Riparian areas with aspen and/or cottonwoods canopy cover.	28

### 3.2. Productivity Estimates

Net primary productivity was estimated using an ecosystem process model, Forest- BGC, (Running and Coughlan 1988; Running and Grower, 1991; Running 1994). The particular version of the model that I used was developed for the Columbia River

Basin ecosystem management project (P. Thornton and J. White, pers. comm.) and is referred to here as CRB-BGC.

This model uses vegetation, topographic, soil type and climate characteristics to simulate nutrient cycling, carbon allocation, and hydrologic routing processes. Vegetation inputs in this model are cover type, leaf area index, structural stage, water use efficiencies, nutrient requirements, and ecophysiological constants describing species-specific photosynthetic capacities. Meteorological inputs are daily maximum temperature, minimum temperature, precipitation, humidity, and short wave radiation. Physical site characteristics are soil depth, soil texture, slope, aspect, and elevation. Because 1989 was a typical year in terms of temperature and precipitation (P. Thornton, pers. comm.), the model was run for climate conditions in that year. Vegetation type and structural stage inputs were taken from field measurements of vegetation type conducted in conjunction with avian census point counts and spatially related to regions of the Landsat scene. Leaf area index (LAI) was derived as a function of the Normalized Difference Vegetation Index (NDVI), which is the ratio of near infrared minus red over near infrared plus red reflectance. Terrain and atmospheric corrections are necessary image processing steps to achieve accurate NDVI calculations. The original TM scene was terrain corrected by Hughes/STX Corporation before delivery to the Wildlife Spatial Analysis Lab, and I performed atmospheric correction based on clear lake reflectance (Jansen, 1986). NDVI was calculated using reflectance values averaged for each region. Vegetation types, that were assigned in the field, were grouped into three categories,

evergreen/coniferous, broadleaf/deciduous, and grassland/cropland, and LAI was determined according to Table 3.

Table 3. Formula and source for calculating LAI based on vegetation type.

Vegetation Category	LAI Formula	Source
Evergreen/Coniferous	$LAI \equiv \left( \frac{NDVI}{0.538} \right)^{6.06}$	Spanner, et al. 1990
Deciduous/Broadleaf	$LAI \equiv \left( \frac{NDVI}{0.26} \right)^2$	Pierce, et al. 1993
Grassland/Cropland	$LAI \equiv (NDVI)1.71 + 0.48$	Asrar, et al. 1984

Physical variables (soil depth and soil texture) were derived from the Montana State Soil Geographic database as prepared for the Columbia River Basin (CRB) ecosystem management project (J. Menakis, pers. com.). I received these data set as an ARC/INFO polygon (vector) coverages and converted it to raster grids. Regions in my study area were overlaid on the CRB soil grids, then depth and texture were recorded as the majority value.

Meteorological variables were extrapolated from daily observations of maximum temperature, minimum temperature, and precipitation recorded during 1989 at National Weather Service and Natural Resources Conservation Service weather stations by using a climate simulation model (Thornton, et al. 1997). A 100-m digital elevation model was used to generate the climate predictions on a daily time step. Observations from weather stations outside the study area were included to ensure accurate predictions at the study area boundaries. Weather station observations were included for stations that had fewer

than 25 days of missing data in each year. Potential evapotranspiration was calculated according to Kimball et al. (in press) using the climate predictions generated for input into CRB-BGC.

### *3.3. Statistical Analysis*

All statistical and graphical analyses were performed on both the entire data set, and on data grouped by vegetation type. Productivity, potential evapotranspiration (PET), and precipitation were each plotted against avian species richness for all points combined, and for each vegetation type separately, as an initial pattern detection step. Graphs are presented for a limited number of vegetation types to conserve space. Bivariate and partial correlations were calculated between productivity and species richness. Partial correlations between productivity and species richness were run holding all vegetation and climate variables, NDVI, and elevation constant. Step-wise multiple regressions were run, including as potential variables productivity, all vegetation variables from Table 1, climate variables, NDVI, and elevation, with the criteria  $p_{in} < 0.05$  and  $p_{out} > 0.10$ . All statistical analyses were performed using SPSS (SPSS, Inc. 1983).

## **4. RESULTS**

### *4.1. Descriptive Statistics and Correlations*

Net primary productivity (NPP) ranged from  $-0.20 \text{ kg C/m}^2/\text{yr}$  to  $1.13 \text{ kg C/m}^2/\text{yr}$  (Table 4). The greatest mean productivity values were in Douglas-fir areas, and the

lowest mean productivity values were in grassland vegetation types. Mean species richness ranged from 3.3 to 9.1 species per point, with highest mean richness in cottonwood vegetation types.

Table 4. Minimum, mean, and maximum NPP and species richness by vegetation type. Number of census points in parenthesis.

Vegetation Type		NPP (kg C/m <sup>2</sup> /yr)			Species Richness		
		min	mean	max	min	mean	max
Cedar/Hemlock	(18)	0.27	0.59	0.80	1	3.3	6
Douglas-Fir	(123)	0.03	0.63	1.01	0	5.0	13
Lodgepole Pine	(90)	0.02	0.47	0.78	0	4.4	11
Ponderosa Pine	(47)	0.00	0.58	1.11	0	4.9	12
Spruce/Fir	(47)	0.00	0.36	0.82	3	7.2	13
Mixed Conifer	(890)	-0.20	0.50	0.97	0	6.5	15
Cottonwood/Aspen	(28)	0.12	0.53	1.04	3	9.1	13
Riparian Shrubs	(117)	0.02	0.52	1.13	2	8.7	17
Grassland	(152)	0.03	0.32	0.58	1	4.7	11
Cutting Units	(681)	-0.11	0.48	1.01	0	6.8	14
All Points	(2283)	-0.20	0.49	1.13	0	6.4	17

A relationship was not evident in scatterplots of productivity versus avian species richness for all points (Fig. 2 ), nor when graphed for separate vegetation types (Figs. 3-5). There was tremendous variation in species richness for all levels of NPP. Low species richness occurred at all levels of NPP, and high species richness also occurred at all levels of NPP.



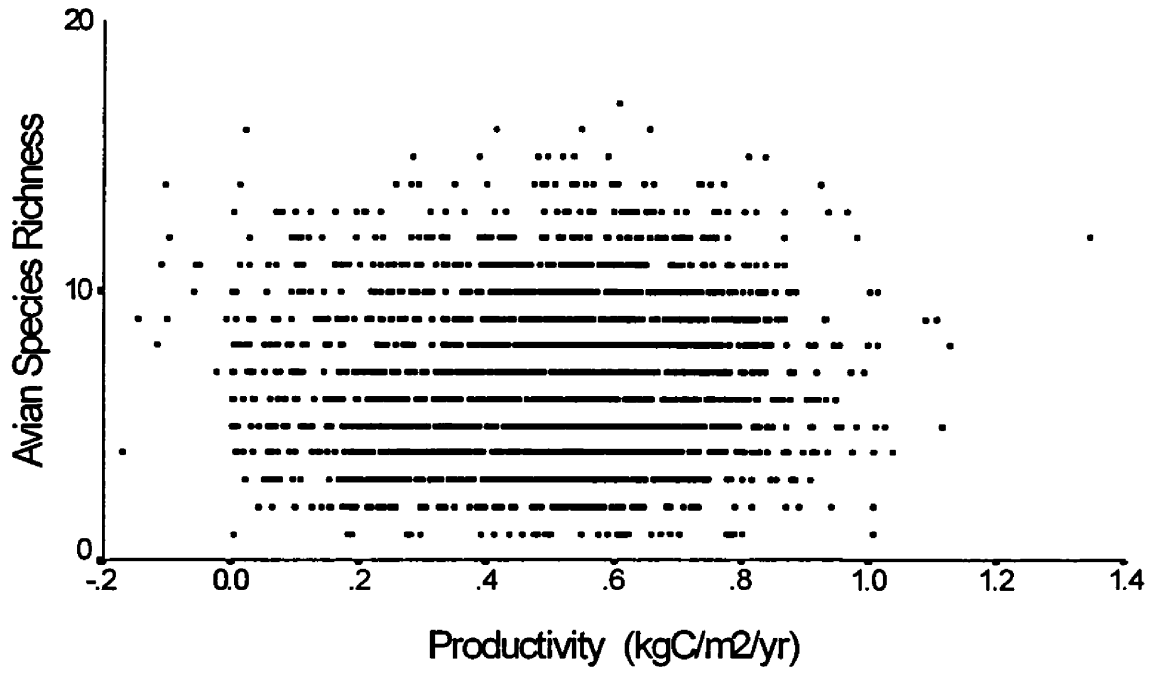


Figure 3. Scatterplot of net primary productivity versus avian species richness for all points. (n = 2283)

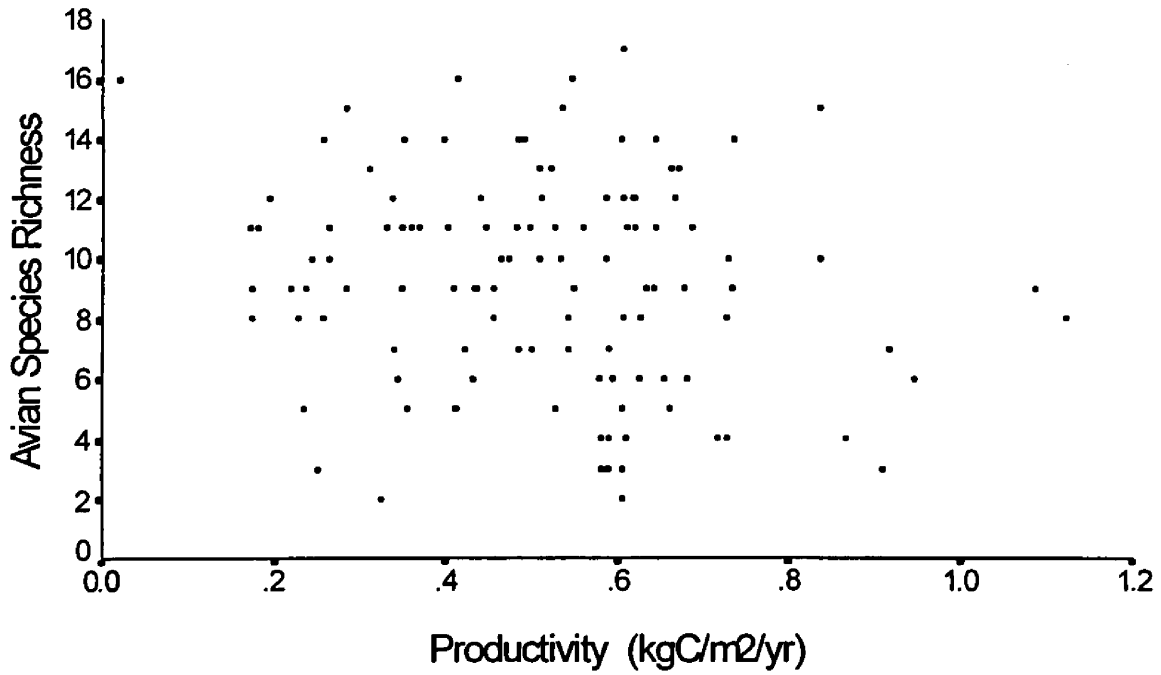


Figure 4. Scatterplot of net primary productivity versus species richness for riparian shrubs. (n = 117)

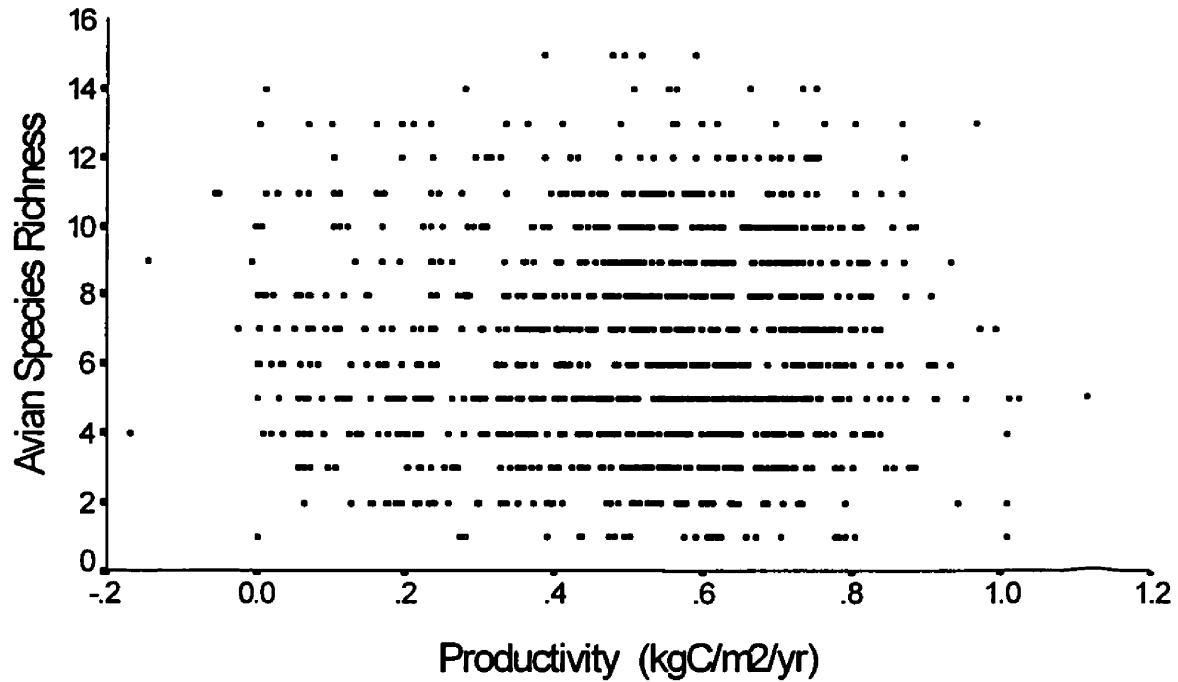


Figure 5. Scatterplot of net primary productivity versus species richness for mixed conifers. (n = 890)

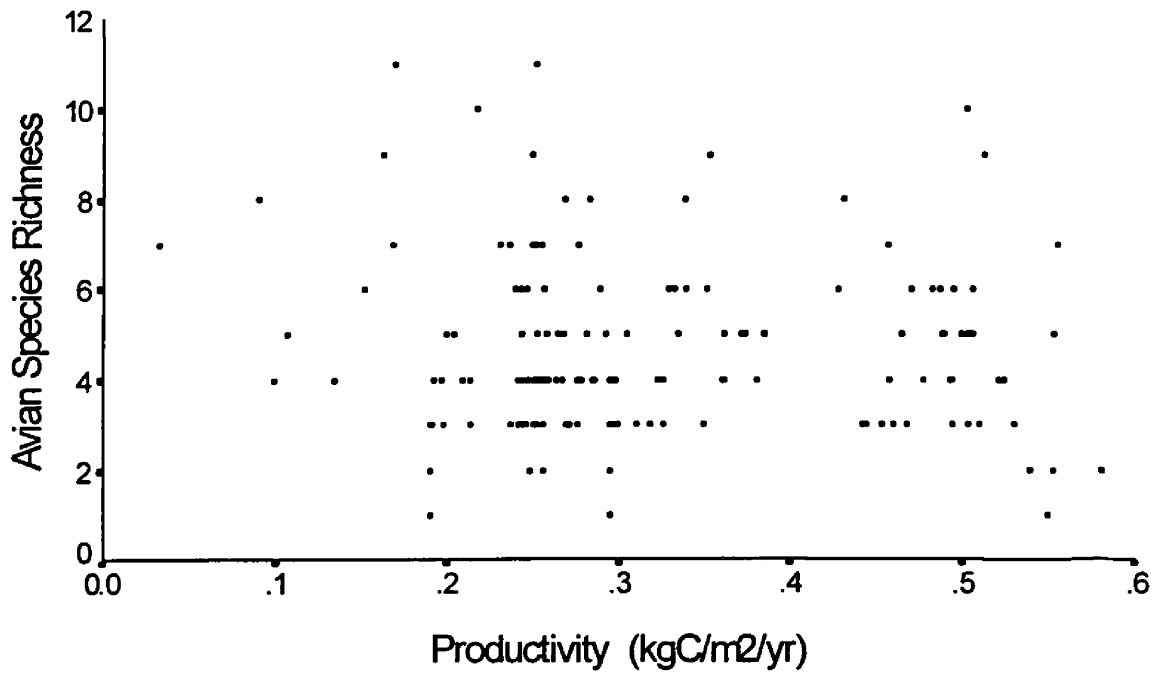


Figure 6. Scatterplot of net primary productivity versus species richness for grasslands. (n = 152)

There was also great variation in species richness given potential evapotranspiration across all points (Fig. 6) and within vegetation types (Fig. 7-9). Precipitation did not show a relationship with species richness when all points were combined (Fig. 10), or when considering vegetation types separately. The correlation between NPP and species richness was exceedingly low in most cover types (Table 5). Productivity was negatively associated with richness in cottonwood vegetation types, but when the effects of other variables were removed, the association was positive, but not significant. A positive bivariate correlation between productivity and species richness was observed for cutting units, but the partial correlation was not significant.

Table 5. Bivariate and Partial correlation coefficients between productivity and species richness. Sample size in parenthesis.

Vegetation Type		Correlation Coefficients	
		Bivariate	Partial
Cedar/Hemlock	(18)	-0.25	-0.16
Douglas-Fir	(123)	0.13	0.06
Lodgepole Pine	(90)	-0.05	-0.01
Ponderosa Pine	(47)	-0.06	-0.09
Spruce/Fir	(47)	-0.02	-0.07
Mixed Conifers	(890)	0.06	0.00
Cottonwoods	(28)	-0.37*	0.23
Riparian Shrubs	(117)	-0.18	-0.02
Grassland	(152)	-0.10	-0.11
Marsh	(52)	0.06	-0.05
Sagebrush	(38)	0.00	0.30
Cutting Units	(681)	0.09*	0.00
All Points	(2339)	0.07*	-0.01

\* =  $p < 0.05$

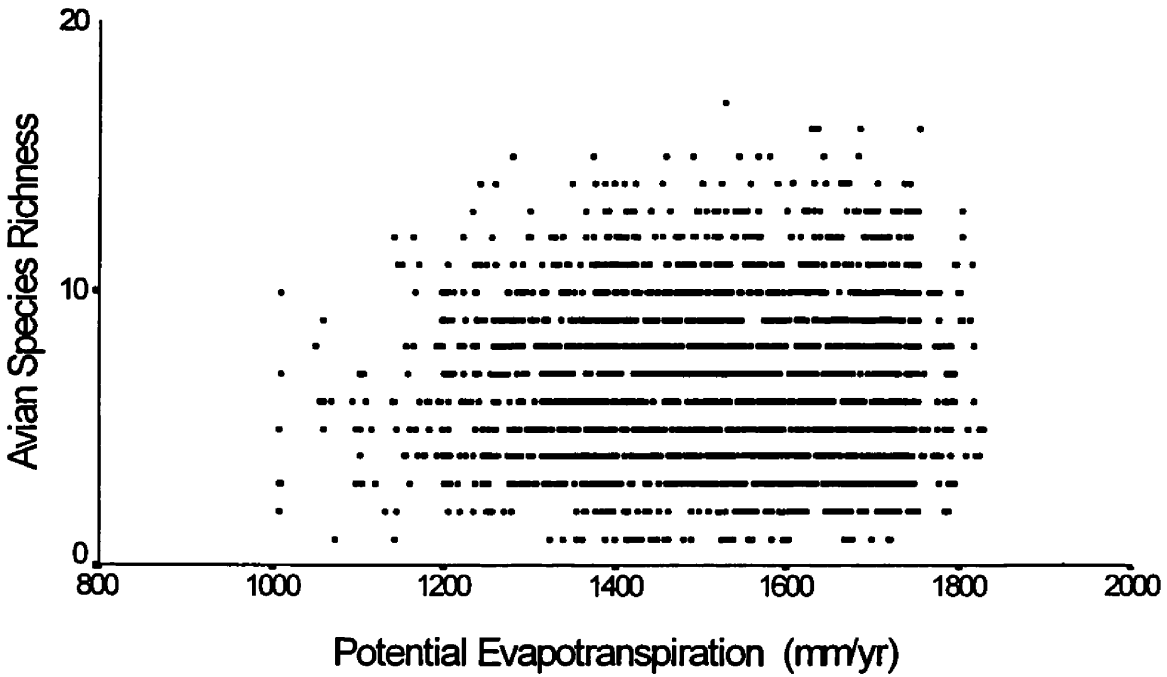


Figure 7. Scatterplot of Potential Evapotranspiration versus avian species richness for all points. (n = 2283)

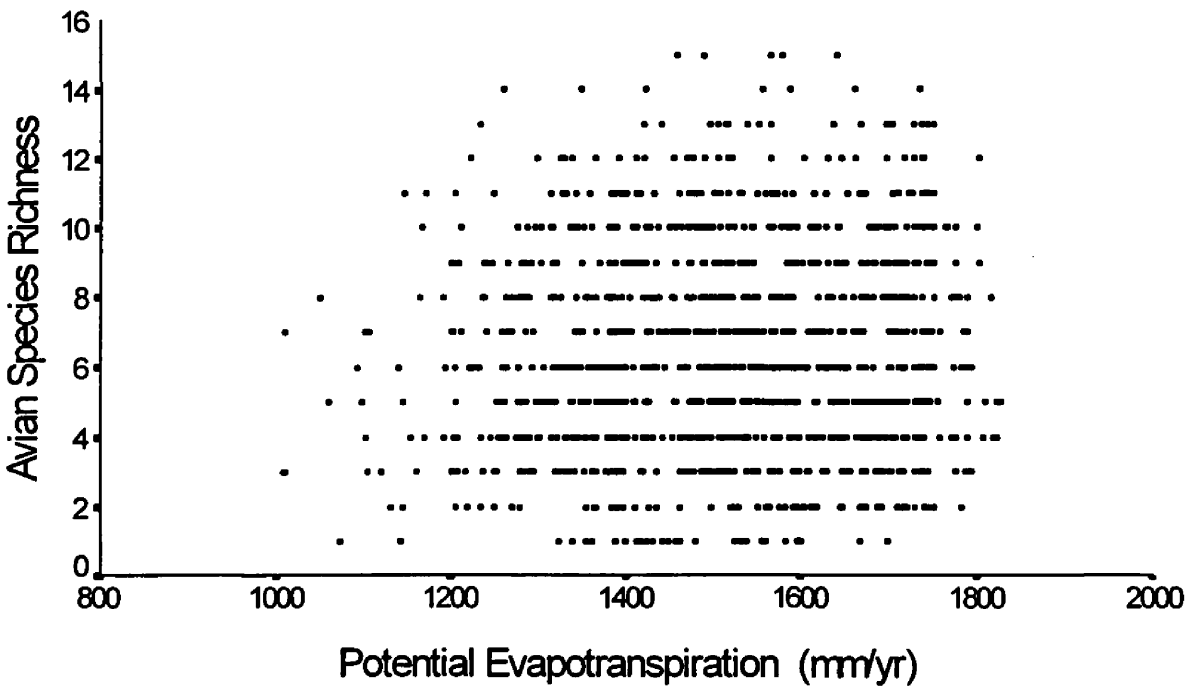


Figure 8. Scatterplot of potential evapotranspiration versus avian species richness for all conifer vegetation types. (n = 890)

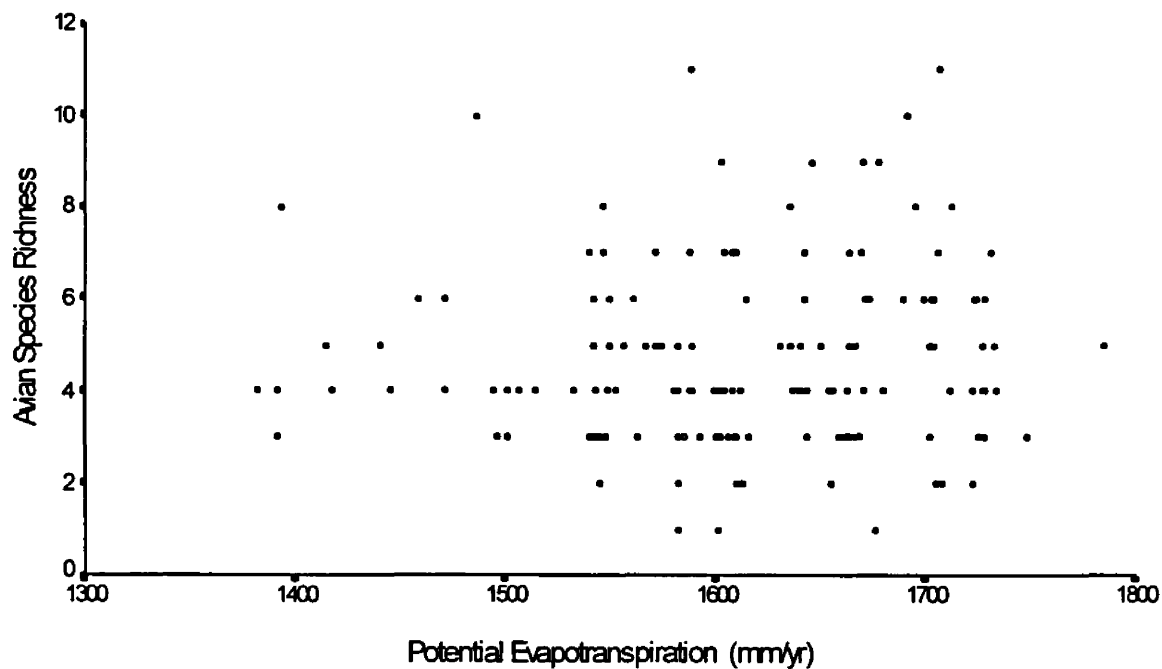


Figure 9. Scatterplot of potential evapotranspiration versus avian species richness for grasslands. (n = 152)

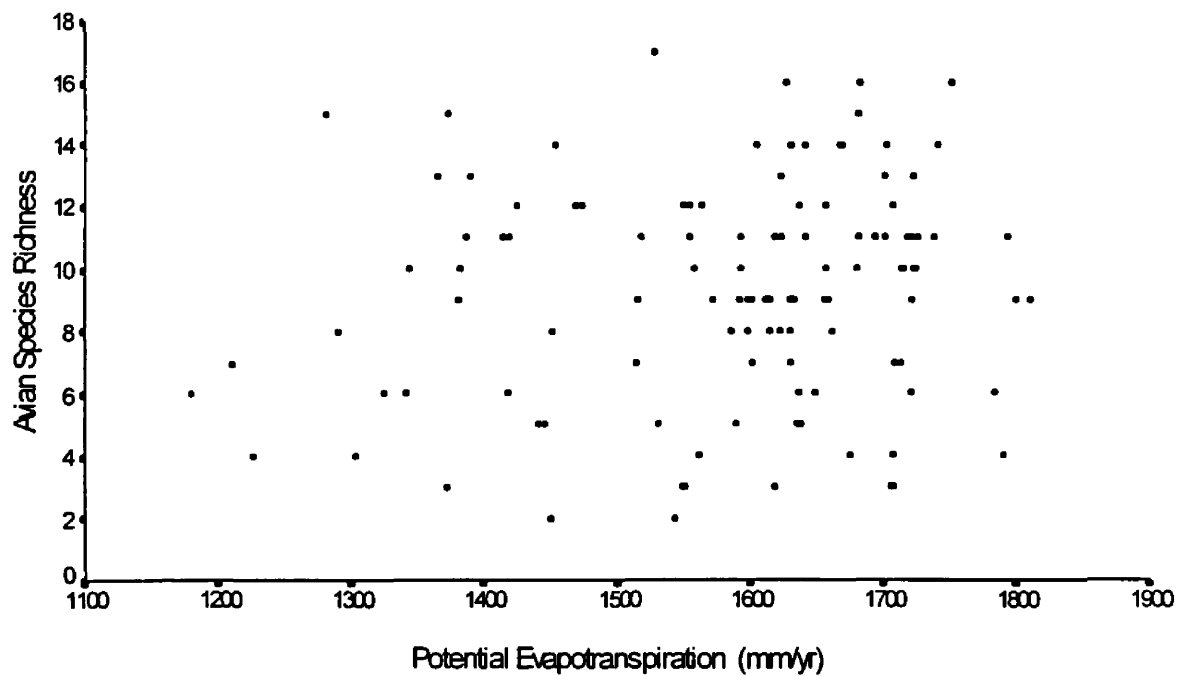


Figure 10. Scatterplot of potential evapotranspiration versus avian species richness for riparian shrubs. (n = 117)

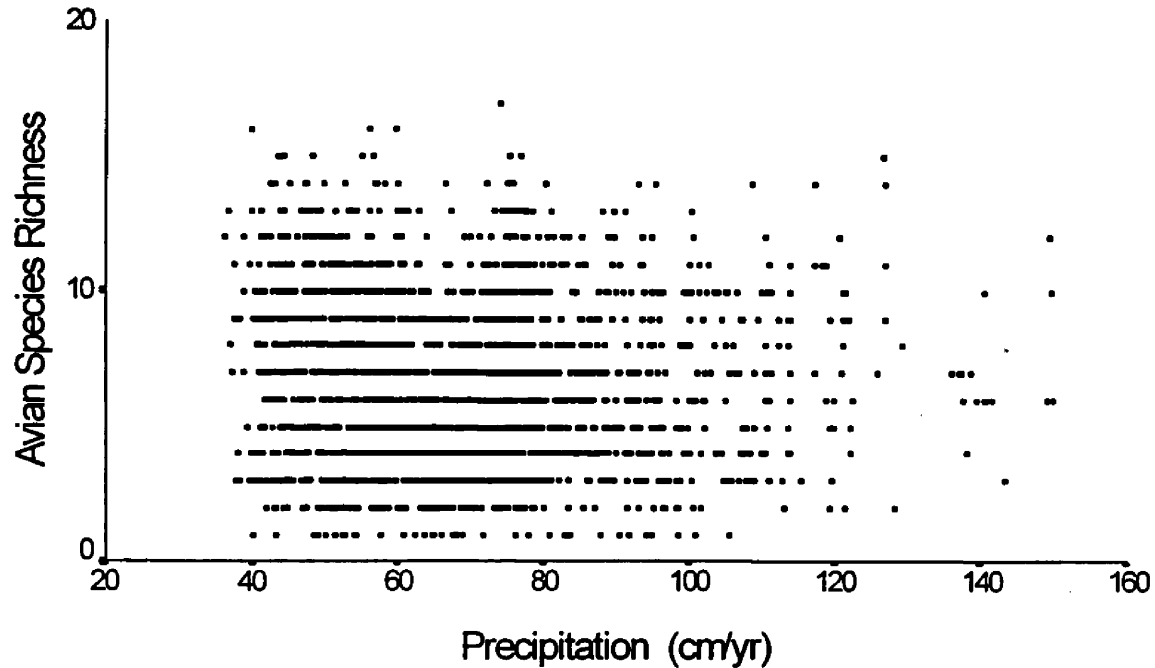


Figure 11. Scatterplot of Precipitation versus avian species richness for all points. (n = 2283)

#### 4.2. Regression Analysis

Productivity was retained as a contributing variable in step-wise multiple regression for Douglas-fir cover types only (Table 6). In all other cover types it was dropped from the equation. Percent herbaceous ground cover was included in all multiple regression equations except for cottonwoods. Other variables commonly included in the regression equations were percent bush and shrub cover, elevation, height of tree canopy, and temperature. Precipitation, percent canopy closure, and the Normalized Difference Vegetation Index (NDVI) also were included, but less frequently.

Table 6. Sign of the constant of variables retained in step-wise multiple regression of species richness and variables shown. All p-values < 0.05. Sample size in parentheses.

Vegetation Type		Variable										R <sup>2</sup>	
		Ground Cover	Shrub Cover	Bush Cover	Elevation	Canopy Height	NDVI	Tmax	Tmin	NPP	PRCP		
Cedar/Hemlock	(18)					-							0.710
Douglas-Fir	(123)	+		+	-					+			0.159
Lodgepole Pine	(90)	+	+										0.070
Ponderosa Pine	(47)	+	+										0.509
Spruce/Fir	(47)			+				+					0.430
Mixed Conifers	(890)	+	+	+	-	-		+	-				0.302
Cottonwoods	(28)				-								0.678
Riparian Shrubs	(117)	+	+					+					0.217
Grassland	(152)	+	+										0.108
Sagebrush	(38)		+					+					0.602
Cutting Units	(681)	+		+	-		+		-				0.232
All Points	(2283)	+	+	+	-		+	+	-		+		0.526

## 5. DISCUSSION

### *5.1. Productivity Estimates*

The ecosystem process model BGC has been tested against field measurements, and net primary productivity estimates were found to have a high correlation with measured values;  $R^2 = 0.82$  (Running 1994). The range of net primary productivity values in this study (Table 4) agrees with values generated by previous BGC simulations for Western Montana (Pierce 1994b.). Negative productivity values can arise from over-estimating leaf area, under-estimating soil water hold capacity, or misidentification of vegetation type. These negative productivity values occurred primarily in cutting units and open forest, where, due to low tree cover, it is difficult to assign the entire area to one

vegetation type. Productivity estimates in this study conform to associations one would expect to find among productivity and other environmental factors. For example, cottonwood vegetation types were the most productive (Table 4), and higher productivity was associated with greater amounts of precipitation. These are not perfect relationships, because additional variation is due to factors such as elevation, soil type, and leaf area. Nonetheless, productivity estimates in this study are most likely representative of the actual pattern of productivity across the study area.

### *5.2. Productivity - Species Richness Relationship*

A positive association between productivity and species richness has been found for some taxonomic groups such as lizards (Pianka 1967) and rodents (Brown 1973, Brown and Davidson 1977) and a negative association for mammals, bats and rodents (Buzas 1972, Fischer 1960, Owen 1990). Still other studies suggest species richness peaks at an intermediate level of productivity (Abramsky and Rosenzweig 1984, Owen 1988). Discrepancies are in part due to comparing results from studies relating plant productivity to plant species richness with studies relating plant productivity to animal species richness. It seems that productivity should influence these two scenarios in fundamentally different ways; in plant-plant scenarios, both productivity and diversity are attributed to the same taxonomic group, but in plant-animal scenarios, it is productivity of one taxonomic group having an effect on the diversity of a different taxonomic group (Rush and Oosterheld 1997). The theory to describe the unimodal relationship that is



often observed between plant productivity and plant diversity is based on nutrients being limiting at low productivity levels, and light being limiting at high productivity levels, and the best competitors taking a greater share of the resources; while at intermediate levels of productivity, neither light nor nutrients are limiting and no species have the competitive ability to exclude others (Tilman and Parala 1993). Nutrient and light supply are not likely to have the same limiting effect on animal populations. Consequently, the following discussion is limited in reference to previous studies that examined the relationship between plant productivity and animal species richness.

My findings do not support a relationship between productivity and avian species richness. Graphical analysis revealed great amounts of scatter, correlation coefficients were low, and productivity was not retained as a variable in multiple regression equations. These results are in striking contrast to previous studies where avian species richness was found to have a strong positive relationship with productivity (Currie 1991), and mammal species richness to be either negatively (Owen 1990). or unimodally related to productivity (Abramsky and Rosenzweig 1984). The fact that I found a lack of relationship between productivity and avian species richness while others have reported a strong relationship between productivity and several taxonomic groups could be due one or more of the following reasons: 1) an inappropriate scale at which NPP was measured in relation to the scale at which richness was measured, 2) methods that did not allow for accurate measurement of predictor and/or response variables, 3) significant differences

between my methods of estimating productivity and the methods used by others, or 4) the lack of a relationship between the two.

One difference between this and previous studies is the scale at which the productivity hypothesis was tested. Many species richness studies were conducted at a broad scale, from continental (Cook 1969, Currie 1990, Schall and Pianka 1978, Simpson 1964), to regional, for example deserts of the western United States (Brown 1973, Owen 1988, Pianka 1967). I tested the productivity hypothesis at a landscape scale, with a study area of approximately 32,000 km<sup>2</sup>. It is likely that diversity at a landscape scale will be influenced by processes different from those acting on a regional or geographical scale (Huston 1994, Ricklefs 1987). For example, density estimates of individual bird species were found to vary with different habitat features depending on the scale at which the relationships were analyzed (Wiens, et al. 1987). Further evidence for scale affecting the results is discussed below in relation to the energy hypothesis as an extension, or alternative to the productivity hypothesis. Determining if scale accounts for the lack of relationship found in this study, will require using these same methods to estimate productivity across a larger area, such as the state or a region including several states, and obtaining similar avian survey data.

Many productivity - species richness studies have been conducted in desert environments where productivity was assumed to be limited by precipitation and therefore was estimated based on annual precipitation, actual evapotranspiration, or potential evapotranspiration (Brown 1973, Owen 1990, Pianka 1967). Although these

methods may be adequate for characterizing productivity over large areas, they do not account for differences in soil type, topography, and microclimate (Box, et al. 1989). I report data on potential evapotranspiration and precipitation for comparison, but I could not use those data by themselves to calculate productivity, and instead used an ecosystem process model that incorporated variables in addition to climatic variables. There has not been a comparison of these methods of estimating productivity and the range of productivity reported here should be compared to that of previous studies only with caution. In most of the studies where productivity was estimated from associated climatic variables, a unimodal relationship was observed between productivity and richness. It is possible that this unimodal relationship is a response to a limiting factor, like precipitation or solar radiation, and not to the productivity gradient. Because many variables exert control on productivity in my study area, there is not a gradient of a single limiting factor that corresponds to the productivity gradient. It would be interesting to see what type of relationship is observed between productivity and richness in arctic regions, where temperature is a strong limiting factor. More work is required to determine if the often observed relationship between productivity and richness is a response to the productivity gradient, or a response to a limiting factor other than productivity.

From the results of this study I conclude that avian species richness is not a function of net primary productivity at a landscape scale. It is possible that species richness in low productivity habitats is maintained by immigration from adjacent habitats

of high productivity. There are, however other variables in this data set that appear to have a relationship with species richness.

### *5.3. Possible Determinants of Species Richness*

Percent herbaceous ground cover had the highest correlation with avian species richness in all vegetation types, except cottonwoods, in this study. Shrub/bush cover, and height to tree canopy were also important. These correlations with habitat structure are in agreement with documented evidence for avian species richness responding to vegetation structure (Lynch and Whigham 1984, Rottenberry and Wiens 1980), particularly foliage height diversity (Karr and Roth 1974, MacArthur and MacArthur 1961, MacArthur 1964, Wilson 1974) and percent herbaceous ground cover (Karr and Roth 1971, Wilson 1974). More complex vegetative structure seems to allow more bird species to co-exist, because some species nest in or feed on herbaceous ground vegetation, while others are associated with shrubs, and still others with tree bark and canopy leaves. Higher ground cover and greater vegetative structural complexity should therefore equate with higher productivity, and if there were a relationship between structural components and species richness, then there should be a relationship between productivity and species richness. Yet I found significant correlations between structural characteristics, but not with productivity. This may be explained by differences between data sets. Productivity was herein estimated using leaf area as detected by satellite, while habitat structure variables (percent herbaceous cover, shrub/bush cover, and height of tree canopy) were measured in the

field at each census point. When the canopy is closed, satellite derived leaf area is a measurement of the top layer of the canopy only, any mid-level or ground level vegetation is not detected. In open canopies, reflectance measured by the satellite is the sum of the reflectance from ground through canopy level vegetation. In this study, leaf area was calculated assuming a homogenous cover of the dominant vegetation type. In other words, there was no partitioning of productivity between tree, shrub and herbaceous compartments. This is because there is not a satisfactory method for partitioning remotely sensed reflectance values into ground, mid, and canopy level leaf area, and the ecosystem process model BGC was designed to make use of remotely sensed data. The development of a remote sensing method for separating ground, mid-level, and canopy reflectance would allow for the partitioning of productivity into ground, shrub, and canopy estimates before testing for a relationship with species richness. It could then be determined if greater vegetative structure did equate with higher productivity, and/or if the productivity of particular vegetation layers influenced species richness.

Forest fragmentation and landscape level habitat characteristics such as patch size and degree of isolation have been shown to influence bird communities (Freemark and Collins 1989; Galli et al. 1976; Lynch and Whigham 1984; Robbins, et al. 1989). Smaller patches of forest tend to support fewer area-sensitive species. Timber harvest in this area of western Montana occurs on public and private land, resulting in a mosaic of forest types and ages. This juxtaposition of patch size and forest types may account for some of the variation in species richness across the productivity gradient. It would be interesting

to examine species richness in western Montana in relation to forest patch size and degree of isolation, then return to test for a relationship between productivity and species richness in sufficiently large or well positioned forest patches. Alternatively, the study could be repeated in an area where timber was not harvested, such as wilderness areas. Since natural disturbances can also create mosaic of forest types and ages, the effect of patch size and degree of isolation would need to be evaluated in wilderness areas as well. This was not done here because avian census data were generally lacking in wilderness areas, and the effect of forest fragmentation was not part of my original hypothesis.

There is some evidence that species richness at broad scales may be related to ambient energy, as measured by potential evapotranspiration (PET). Currie (1991) examined patterns of species richness among vertebrates across North America and found that avian species richness peaked, then declined after an intermediate level of productivity, but remained constant after reaching a maximum at an intermediate level of potential evapotranspiration. He suggested that because potential evapotranspiration is a measure of ambient energy, animals may be responding to energy sources unrelated to productivity. I did not find evidence of the same strength of relationship. There was large variation in avian species richness given PET, but the rather distinct edge along the upper limits of species richness suggest maximum species richness may be limited by potential evapotranspiration. A relationship between avian species richness and potential evapotranspiration rather than productivity, would support Currie's hypothesis that vertebrates are responding to energy sources unrelated to the energy fixed as primary

productivity. This energy could be in the form of ectotherms, which might prosper in higher ambient energy environments.

That PET appeared to confine the maximum possible avian species richness leads me to believe the scale of analysis in my study was at least partially responsible for the differences reported here versus past studies. The same limits of maximum species richness are present, though less distinct, in graphs of productivity versus species richness. When either productivity or potential evapotranspiration is related to species richness within a vegetation type, the relationship diminishes even further. This suggests the differences between my results and those of broad-scale studies may be due to the scale at which the hypothesis was tested and that my study was conducted using data at the lower limit of resolution at which an effect can be detected.

Specific habitat features such as snags, cliffs, or streams are critical for the presence of some bird species. These may be distributed unevenly in relation to the productivity gradient and have the effect of increasing variation in the pattern of species richness. Likewise birds may be temporarily attracted to areas where insect outbreaks are occurring, or a seed crop is ripe. These sorts of area and time specific features can alter the number and composition of species in a census, and obscure an otherwise valid relationship with other variables. In this case, however, because census data were combined from four different years, the effect of such variation should be minimal. If those conditions were obscuring a relationship with productivity, they should also

obscure other relationships, yet ground cover and structural diversity were clearly significant factors.

Although avian species richness was not significantly influenced by productivity, it may be that other measures of the avian community are. Community composition at census points with high productivity was less similar than that at points with low productivity. As these results were not rigorously tested, and it remains to be seen if in fact there is greater variation in species composition in high productivity habitats than in low productivity habitats. If so, this could indicate that a few species have greater competitive ability in low productivity habitats, but when productivity increases, competition becomes less important, because the same species do not always appear in those places. This is purely speculative and deserves specific attention; I suggest it as a possibility based on preliminary findings. Finally, it is also possible that productivity regulates the total amount of avian biomass that can exist in a habitat. Because the census methods used in this study were designed to detect the presence or absence of bird species, the actual abundance data necessary to investigate this hypothesis were not available.

#### *5.4. Conclusions*

I have shown that in western Montana, it is not possible to predict avian species richness from net primary productivity. As described above, there is still work to be done to determine productivity estimates of multiple canopy layers would allow for such a



prediction, or if there is no a relationship between productivity and avian species richness at the landscape scale. Given the strong relationship between herbaceous and shrub ground cover with species richness, a method that enables reflectance to be partitioned into ground, shrub, and canopy level leaf area, and modeled as such, is urgently needed. Even if further studies show no relationship between productivity of separate canopy levels and species richness, the ability to monitor changes in ground, mid-level and canopy level vegetation cover would be a powerful indicator of habitat suitability. Because potential evapotranspiration and landscape heterogeneity exhibit a strong relationship with species richness, and because these variables are readily detectable through remote sensing, future studies should evaluate the potential of using these factors for mapping and monitoring biological diversity.

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