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Environmental correlates of avian species richness over southern Ontario, Canada.

Michael René Muller

Thesis submitted to the
School of Graduate Studies and Research,
University of Ottawa

in partial fulfillment of the requirements for the
Master's of Science (M.Sc.) degree in the
Ottawa-Carleton Institute of Biology

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The many people that have made a difference during this time,
you know who you are...
I've talked with you, laughed with you, hugged you, helped you, made you cookies or,
bought you a beer...
Hopefully, I got around to telling you how much you matter to me.

Thanks.

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ABSTRACT

Species richness is an ecologically important descriptor of ecosystems and, as a component of biodiversity, may be useful for conservation planning.

Global and local patterns of richness have been related, with moderate success, to climatic and habitat parameters respectively. However, our ability to predict species richness breaks down at intermediate scales (quadrats 10^0 - 10^3 km^2 in size extending over regions of 10^3 - 10^6 km^2).

We examined the spatial variation in breeding bird species richness in 100 km^2 squares, across 200 000 km^2 of southern Ontario, and tested for relationships with a suite of environmental variables that included, climate, human population, land cover, a heterogeneity index, soil fertility and parkland. Even though many of the climatic and land cover measures were significantly related to total avian species richness, none of the predictors accounted for more than 14% of the variation in richness. Temperature and total forest cover explained the greatest amount of variation in species numbers across southern Ontario.

The number of observer hours spent per square varied over the study area and covaried with both the measures of species richness and several of the characteristics of the environment. Statistically controlling for the effect of observer hours did not alter any of our qualitative conclusions. We also removed the effects of temperature from the total avian species richness - environment relationships, which altered many of the trends observed.

We then classified each of the species according to various life-history characteristics and examined the relationships between the variation in richness of these groups (guilds) and the environmental variables. Up to four times as much of the variation in guild richness can be explained using single environmental variables, than is the case for total avian species richness. The amount of variation explained depends on the life-history guild chosen.

Conifer nester richness and building nester richness were much more strongly related to environmental characteristics than the richness of other nesting guilds and those based on migratory strategy. The variation in richness of coniferous nesters and long distance migrants was most strongly related to total forest cover.

Building nesters were, not surprisingly, strongly related to human population and the number of occupied dwellings in a UTM square. The richness of the rest of the life-history guilds, like total avian species richness, was most closely related to measures of temperature.

We conclude that at this spatial scale, the variation in total avian species richness over southern Ontario is not sufficiently well related to either temperature or habitat to warrant further investigation of possible mechanistic links. The richness of certain guilds, however, shows some promise as a possible measure for conservation planning and management. We suggest further investigation of which life-history traits are appropriate for guild classification, and the specific habitat types associated with the richness of those guilds.

M. R. Muller - Avian speicies richness over southern Ontario

RÉSUMÉ

La richesse spécifique représente une caractéristique fondamentale des écosystèmes. En tant que composante de la biodiversité, la richesse spécifique est très importante pour des fins de gestion.

Des travaux scientifiques antérieurs ont déjà bien décrit les distributions spatiales de la richesse spécifique, sur l'échelle globale ainsi que sur l'échelle locale. On a mis en évidence que ces distributions sont assez bien corrélées avec des facteurs climatiques (surtout à grande échelle) et des caractéristiques de l'habitat (surtout à petite échelle). Pourtant, aux échelles intermédiaires (dans des quadrats dont la superficie varie de 10^0 à 10^3 km^2, étalés sur des régions de 10^3 à 10^6 km^2), on a moins bien réussi à expliquer la variabilité spatiale de la richesse spécifique.

Dans l'étude actuelle, on a examiné la variabilité spatiale de la richesse spécifique des oiseaux nicheurs dans le sud de l'Ontario. On a utilisé un système de quadrats ayant une superficie de 100 km^2 chacun, répartis sur une aire de 200 000 km^2. Par la suite, on a corrélé cette variabilité avec une suite de variables environnementales incluant le climat, la population humaine, le type de végétation, un indice de l'hétérogénéité des types de végétation, la fertilité du sol, et la superficie des parcs.

Bien que la richesse spécifique soit corrélée avec plusieurs de ces caractéristiques environnementales, aucune de ces dernières n'a statistiquement expliqué plus de 14% de la variabilité en richesse spécifique. La température et l'aire totale de forêt se sont avérées les variables les mieux corrélées dans le sud de l'Ontario.

L'intensité de l'échantillonnage variait d'un quadrat à l'autre, et elle co-variait avec les mesures de la richesse spécifique ainsi qu'avec plusieurs des variables environnementales.

L'intensité de l'échantillonnage variait d'un quadrat à l'autre, et elle co-variait avec les mesures de la richesse spécifique ainsi qu'avec plusieurs des variables environnementales. Peu importe si on contrôle statistiquement l'effet de l'intensité d'échantillonnage ou pas, on tire essentiellement les mêmes conclusions. De façon analogue, on a statistiquement enlevé l'effet de la température afin d'examiner les corrélations partielles entre la richesse spécifique et d'autres variables. Ceci a eu pour effet de modifier la forme de plusieurs corrélations.

Par la suite, on a classifié chacune des espèces d'oiseaux selon des caractéristiques de leurs modes de vie (telles que les habitats où elles nichent et leurs stratégies migratoires). Les corrélations entre les variables environnementales et la richesse spécifique de ces groupes d'espèces (guildes) étaient souvent plus fortes que celles avec la richesse spécifique totale. Dans certains cas, les corrélations étaient jusqu'à quatre fois plus fortes, selon la guilde en question.

La richesse spécifique de la guilde des espèces qui nichent dans des conifères, ainsi que celle des espèces qui nichent dans des bâtiments, démontraient des corrélations plus fortes avec des caractéristiques de l'environnement que la richesse d'autre guildes nicheuses et migratoires. La variable environnementale la plus importante était l'aire totale des forêts dans le cas d'espèces qui nichent dans des conifères. Comme on pouvait s'y attendre, la richesse des espèces qui nichent dans des bâtiments dépend fortement de la population humaine ainsi que du nombre d'habitations dans le quadrat. La richesse des autres guildes, comme la richesse totale, est significativement reliée à la température.

En conclusion, à cette échelle spatiale dans le sud de l'Ontario, la variabilité de la richesse spécifique totale ne dépend que faiblement des caractéristiques environnementales citées dans des études antérieures. Il est peu probable qu'elle soit utile pour des fins de gestion. Pourtant, la richesse des guildes est plus prometteuse dans cette optique. Il serait intéressant de faire une investigation plus poussée afin d'identifier des modes de vie qui définissent des guildes pour lesquelles la richesse est fortement reliée aux caractéristiques particulières de l'environnement.

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PREFACE

A piece of research can only contribute to science if it is communicated to others. With that in mind, the organisation of this thesis is oriented around two papers, Chapters III and IV, that are written in a form intended for submission for journal publication. Necessarily, there is some repetition of material as each paper is meant to be able to stand on its own.

CHAPTER I - INTRODUCTION

Rationale

Early ecologists remarked that there were more species in some areas than in others and the explanation of this phenomenon remains one of the pre-eminent ecological questions of the twentieth century (May 1986). The present study examines the spatial variation of the number of bird species, or species richness (McIntosh 1967), over southern Ontario, Canada, and assesses which characteristics of the environment could be responsible for the variation observed.

A first step in the process of determining which factors might influence the number of species in an area is to describe the variation in species numbers across space. Patterns in species richness can be quite different according to both the taxonomic group being studied and the spatial scale at which the organisms are surveyed.

Once the spatial variation of species richness has been described, the observed patterns can then be related to those characteristics of the environment hypothesised to influence species richness. Environmental characteristics that do not covary with species richness can be rejected as possible determinants of the number of species in an area. Experimental manipulation of those factors that do prove to be related to richness can then test whether causal links exist.

Species richness can also vary across time. The introduction of new species through immigration and speciation, as well as the removal of species through extinction, can all contribute to changes in richness. We necessarily assume that the present patterns of species richness are related to current environmental conditions. Furthermore, any temporal changes in species richness that occur introduce only random error into the spatial patterns of richness.

Background

Species richness has been found to covary with different variables according to both the taxonomic group studied and the spatial scale examined (Ricklefs and Schluter 1993a, Huston 1994). Many hypotheses have been proposed to explain these different spatial patterns in species richness (reviewed by Rohde 1992). These hypotheses suggest that the following factors might influence the number of species occurring in an area: history (e.g. Ricklefs 1987), climate (e.g. Schall and Pianka 1978), climatic variability (e.g. Connell and Orias 1964), energy (e.g. Wright 1983, Wright *et al.* 1993), habitat heterogeneity (e.g. Roth 1976), competition (e.g. Pianka 1966), predation (e.g. Paine 1966, Menge and Sutherland 1976) and disturbance (Connell 1975, Huston 1979). There is evidence that most of these elements could indeed influence species richness, at least to some extent, on some spatial scales (Begon et al. 1990, Huston 1994).

On global scales (quadrats of 10^4 - 10^5 km^2 in size, extending over continents) there is a great deal of evidence that climate is strongly related to patterns of species richness. Large scale variation in plant species richness is positively related to actual evapotranspiration (AET) (Wright 1983, Adams and Woodward 1989), statistically explaining 84% of the variation in tree species richness over North America (Currie and Paquin 1987). AET incorporates both the energy and moisture components of climate, since it measures the amount of water evaporated from a given area, given the amount of water available for evaporation. AET has also been shown to be strongly correlated with patterns of primary productivity on large spatial scales (Lieth 1975, Rosenzweig 1968).

Among animals, 69% - 95% of the variation in richness of the Classes of North American vertebrates can be statistically explained by annual potential evapotranspiration (PET) (Currie 1991). In contrast to AET, PET is solely a measure of environmental heat, unconstrained by water availability. It is not clear why PET, "a measure of integrated, crude ambient energy", is more closely related to vertebrate richness than AET, but environmental effects on metabolic rates and the possible creation of additional niches not related to primary productivity are two possible explanations (Currie 1991).

Global patterns in the number of bird species are also strongly related to measures of environmental heat. The equatorial-polar gradients of species richness associated with latitude have been more accurately described using several co-varying measures of heat, especially potential evapotranspiration (PET) (Wallace 1878, Simpson 1964, Wylie and Currie 1993). Specifically for the Aves, 68.9% of the variation in the species richness over North America can be explained by PET (Currie 1991). At large spatial scales, there are generally more species of birds in those areas with higher PET.

Turner *et al.* (1988) tested for a heat - avian richness link, by hypothesising that there should be changes "in species numbers [across Great Britain] according to the seasonal fluctuation in the distribution of available energy". The number of year-round resident bird species in Great Britain was correlated with the variation in seasonal temperatures (winter, summer, spring) and with temperature range (Turner *et al.* 1988).

Furthermore, the number of bird species visiting in summer and winter were each correlated with the variation in temperature of their respective seasons (Turner *et al.* 1988). The authors conclude that their findings support a link between species richness and environmental energy on larger spatial scales (however, problems do remain: they do not satisfactorily explain why the most important correlates of summer resident richness and summer visitor richness are latitude and altitude respectively).

While energy may determine the gross, global patterns of species richness, on the local scale (quadrats 10^{-2} - 10^{0} km^2 in size extending over 10^{0} - 10^{3} km^2 areas), variation in species richness has been primarily attributed to changes in habitat availability. On finer spatial scales, a wide range of factors has been associated with patterns of species richness in many taxonomic groups. For example: the species richness of freshwater molluscs and macrophytes is related to substrate size in Lake Erie (Bailey 1988), the richness of gastropods is related to the cation concentration of the water in English lakes (Savage and Gazey 1987), the richness of coral fish species richness is related to water depth and substrate size (McGehee 1994), the richness of insects is related to plant habitat architecture (Straw and Ludlow 1994), and the richness of small mammals in Australian heathlands is related to habitat heterogeneity (Fox 1981).

Avian species richness on local scales (quadrats 10^{-2} - 10^{0} km^2 in size extending over 10^{0} - 10^{3} km^2 areas) has been consistently related to aspects of vegetation (e.g. Freemark and Merriam 1986, Roth 1976, Urban and Smith 1989). Across eastern North America, the amount of forest cover in an area has repeatedly been found to be the most significant correlate of the number of bird species found there (e.g. Galli et al. 1976, Whitcomb et al. 1981, Ambuel and Temple 1983, Schmiegelow and Nudds 1987, Villard *et al.* 1989). In addition to total forest area, local scale avian species richness has also been associated with internal characteristics of the forest such as vegetation structure, tree/shrub species, canopy height, tree basal area and foliar magnesium (MacArthur and MacArthur 1961, Cody 1981, James and Warner 1982, Braithwaite et al. 1989).

Few attempts have been made to examine richness - environment relationships at intermediate or regional scales (quadrats 10^0 - 10^3 km^2 in size extending over regions of 10^3 - 10^6 km^2). The lack of regional scale studies on avian species richness is largely due to logistical difficulties involved in obtaining appropriate data. Simply censusing all the species in a region, with due accuracy and resolution, is an undertaking involving thousands of person-hours.

Although exploring regional scale richness - environment relationships is resource-intensive, they can be particularly important from a management point of view, since it is at these scales that many civil administrative units (counties, townships and regional municipalities) make conservation and management decisions. Information on which alterations to the physical environment result in changes in species richness can be incorporated into decisions regarding land use zoning and infrastructure construction.

Regional scale richness - environment relationships are also important because the variation in species richness is related to different variables on local and global scales (i.e. appears scale-dependent) and we would like to know at what intermediate spatial scale(s) these relationships change. Do the global richness - climate relationships get weaker and the richness - habitat relationships get stronger as one examines finer spatial scales? Or is species richness related to some other variable(s) at intermediate scales? At what intermediate scale do the relationships change?

Lacking the resources to sample regional scale phenomena effectively, regional scale studies often increase the extent, but not the resolution of their sampling effort. In one of the few regional scale studies, Wiens *et al.* (1987) attempted to quantify avian habitat occupancy patterns over two areas of ~100 000 km^2 and ~2 000 000 km^2 using only 14 sample sites (0.18 km^2 each) and 16 sample sites (0.18 km^2 each), respectively. While they did not examine species richness, various characteristics of the vegetation were related to the abundance of many species (Wiens *et al.* 1987). They also concluded that regional scale studies need a large number of local samples in order to be able average out local effects (Wiens *et al.* 1987).

To investigate richness - environment relationships on a regional spatial scale we examined the species richness of birds over the southern part of Ontario, Canada and we related this variation to a group of environmental variables that are thought to influence richness. Data contained in The Atlas of the Breeding Birds of Ontario (Cadman *et al.* 1987, see Methods), describing bird distributions in 100 km^2 UTM squares over 200 000 km^2 of southern Ontario, permitted the study of regional scale richness - environment relationships, often pre-empted by a lack of appropriate species richness information. Specifically, we tested the following hypotheses: that the number of bird species in 100 km^2 quadrats over southern Ontario is related to climate (measures of temperature and precipitation), land cover (forest cover and type, agriculture, urban area...), human population, parkland, land cover diversity and soil fertility.

These hypotheses generated several testable predictions. Firstly, one would expect to see a positive relationship between avian species richness and surrogates for available energy (e.g. temperature, soil fertility) if energy influences the number of species in an area. Likewise for habitat availability, one would expect to see increased species richness in those areas with increased habitat (insofar as it can be measured through changes in land cover). In addition, one might expect to observe a negative relationship between avian species richness and indicators of possible habitat degradation like human population and the amount of urban area.

CHAPTER II - METHODOLOGY

Preface

When testing hypotheses about richness - environment relationships on regional spatial scales the largest obstacles involve data availability and compatibility. The majority of what follows are solutions to those fundamental problems.

In order to be able to test hypotheses relating the species richness to measures of the environment, one must first find datasets with the appropriate extent and resolution. In addition, a method must be developed for integrating point, vector and areal data into a format that can be queried or sampled prior to statistical analysis.

Species Richness Data

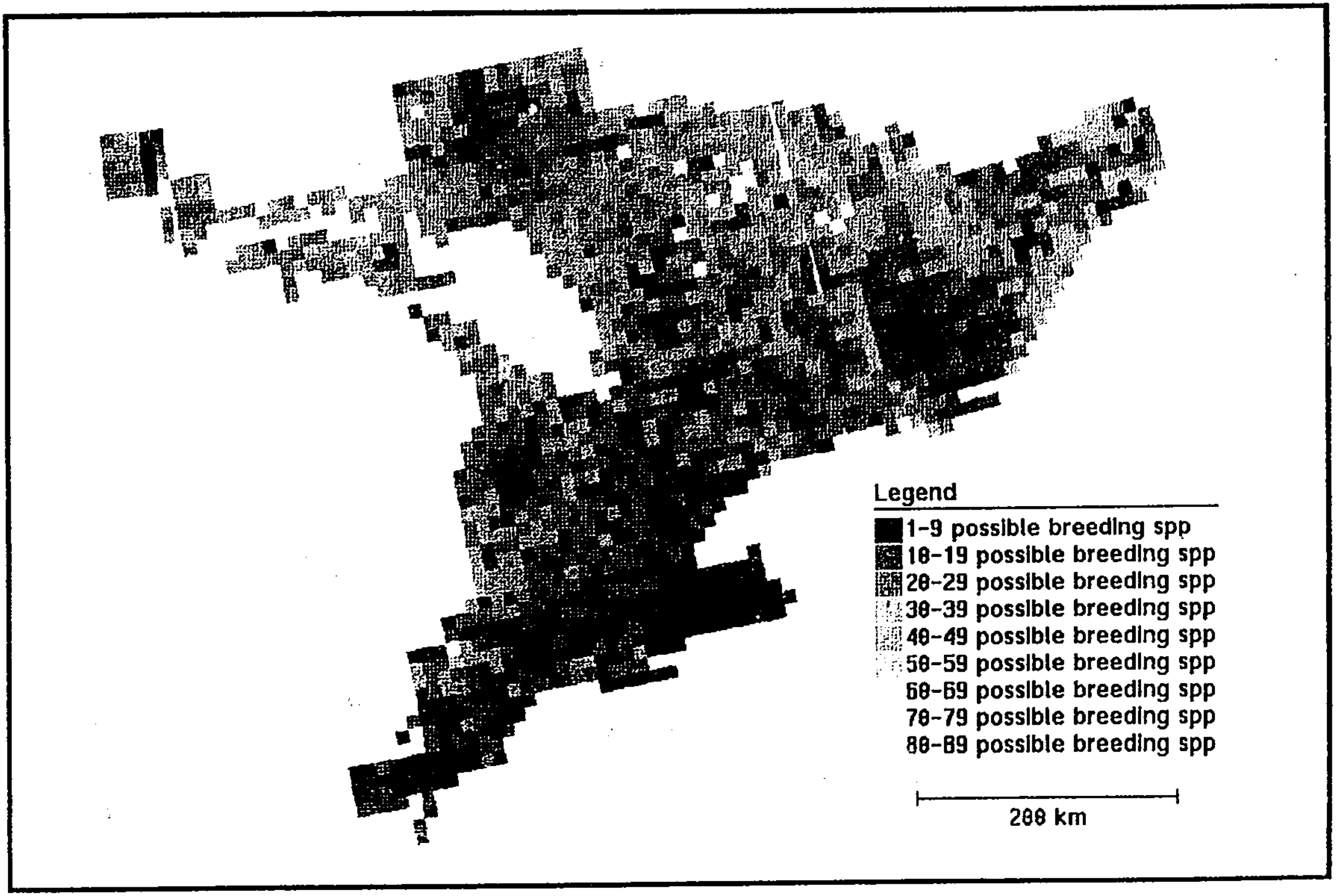
The bird species distribution information that forms the numerical base for The Atlas of the Breeding Bird of Ontario provided one of the best databases available to test for relationships between the number of bird species and measures of the environment on intermediate spatial scales (see Cadman *et al.* 1987). The ABBO database contains presence/absence records for each of the bird species occurring in 10 km by 10 km (UTM squares) extending over the southern portion of the province of Ontario, Canada. This area extends approximately from 42 to 47 degrees north latitude and between 74 and 85 degrees west longitude.

The data for The Atlas of the Breeding Birds of Ontario were assembled using an extensive network of "bird-watchers" to census avian species' presence and absence over southern Ontario (Cadman *et al.* 1987). The use of volunteers incurred certain inevitable errors, inconsistencies and biases, which were mitigated as much as possible through verification of sightings and the recording of observer hours per UTM square (Cadman *et al.* 1987 p19). We did not include those UTM squares with fewer than ten hours of observer effort in the analysis.

Species observations were classified according to 17 sighting criteria assessing the likelihood that the individual bird observed was, in fact, breeding in that particular square (Cadman *et al.* 1987). Based on these criteria, each species observation was recorded as either: "species observed", "possible breeding", "probable breeding" or "confirmed breeding" based on the strength of breeding evidence. To estimate richness, we calculated the number of bird species in each UTM square using the top two and the top three breeding categories. Including only "confirmed" and "probable" breeding records minimised errors related to the observation of non-breeders (transients). However, more remote areas had fewer observer hours and more species classified as "possible breeders" (Figure II-1). This was likely due to atlassers being unable to accrue additional breeding evidence due to physical or time constraints (D. Hussell, Canadian Wildlife Service, personal communication). As a result, including 'possible breeders' in the richness calculations decreased the correlation between sampling effort (the number of observer hours) and species richness and those results are preferentially reported hereafter.

The ABBO data were condensed into a presence/absence matrix of 1721 squares by 232 species. This matrix was then used to calculate the total avian richness per UTM square.

Figure II-1. The spatial distribution of the number of 'possible breeding' bird species in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study.


Legend
1-9 possible breeding spp
10-19 possible breeding spp
20-29 possible breeding spp
30-39 possible breeding spp
40-49 possible breeding spp
50-59 possible breeding spp
60-69 possible breeding spp
70-79 possible breeding spp
80-89 possible breeding spp
200 km

We also classified each species into life history guilds based on migratory strategy and preferred nesting habitat from information contained in compendia by Ehrlich *et al.* (1988), Gauthreaux *et al.* (unpublished) and Farrand (1983). Species were differentiated as either long-distance migrants, (wintering south of the Gulf of Mexico) or as residents/short-distance migrants. Nesting guilds were based on the types of habitat in which nests were commonly found. Each species was associated with one or more of the following nesting habitats: tree snags, coniferous forest, deciduous forest, shrubs (including grass), ground (including floating, cliffs and banks) and buildings (Ehrlich *et al.* 1988). The guild classification of the each of the bird species observed over southern Ontario is found in Appendix A.

Data on Environmental Characteristics

The predictor variables in this study are measurable aspects of the environment that represent many of the factors that have been hypothesized to affect the number of species in an area. Measures of climate, human population, infrastructure, fragmentation, land cover and vegetation have all been included in this study. The specific predictor variables are outlined in Table II-1.

The data on environmental parameters were obtained from several sources. Information on land cover was obtained from National Oceanic and Atmospheric Administration (NOAA) Advanced Very High Resolution Radiometer - Local Area Coverage (AVHRR LAC) digital land cover images interpreted and classified by the Manitoba Centre for Remote Sensing (Lowe *et al.* 1990). The final image of Ontario had

Table II-1. The mean, standard deviation (S.D.), minimum (Min) and maximum (Max) for avian species richness and each of the environmental variables related to it in 10 km by 10 km squares over southern Ontario, Canada. N=1721.

Variable	Mean	S.D.	Min	Max
Total avian species richness	92	16	21	146
Temperature:				
mean annual temperature (°C)	5.7	1.5	3.1	9.7
number of days/year with a maximum temperature of 0°C	285	14	254	320
number of days/year with a minimum temperature of 0°C.	196	18.5	159	247
mean annual daily maximum temperature (°C)	10.9	1.16	8.3	14.4
mean annual daily minimum temperature (°C)	0.4	2	-3.3	5.8
Number of days/year with over 5cm of snow cover	91.3	30.1	19	134
Precipitation:				
total annual precipitation (cm)	89	8.6	67.4	115.9
number of days/year with precipitation	134.6	17	79	179
total annual rainfall (cm)	68.3	6.1	49.4	87.2
number of days/year with rainfall	93.6	9.4	60	124.5
total annual snowfall (cm)	20.8	6.4	7.7	43
number of days/year with snowfall	46.7	13.7	14	85
Soil fertility (total exchangeable bases) (meq/100g soil)	13.7	13.7	1	70
Land Cover*:				
total forest area (km^2)	52.2	40	0	110.7
coniferous forest area (km^2)	1	5.2	0	68.5
mixed forest area (km^2)	44.7	37.5	0	110.7
deciduous forest area (km^2)	6.4	14	0	95.2
agricultural land area (km^2)	33.6	39.2	0	105.6

surface water area (km^2)	12.6	23	0	103.3
built-up area (km^2)	1	6.9	0	90.9
Number of forest classes	1.2	0.7	0	3
Number of land cover classes	2.3	0.8	1	5
Heterogeneity (Shannon-Wiener Index)	0.7	0.5	0	1.9
Park area (ln(ha))	1.6	2.8	0	10.5
Human population (ln)	5.1	3.6	0	13.1
Number of occupied dwellings (ln)	4.3	3.2	0	12.2
Observer hours (ln)	3.7	0.7	2.3	6.8

* due to irregularly shaped UTM squares along the boundary of UTM zones, several squares were slightly larger than 100 km^2.

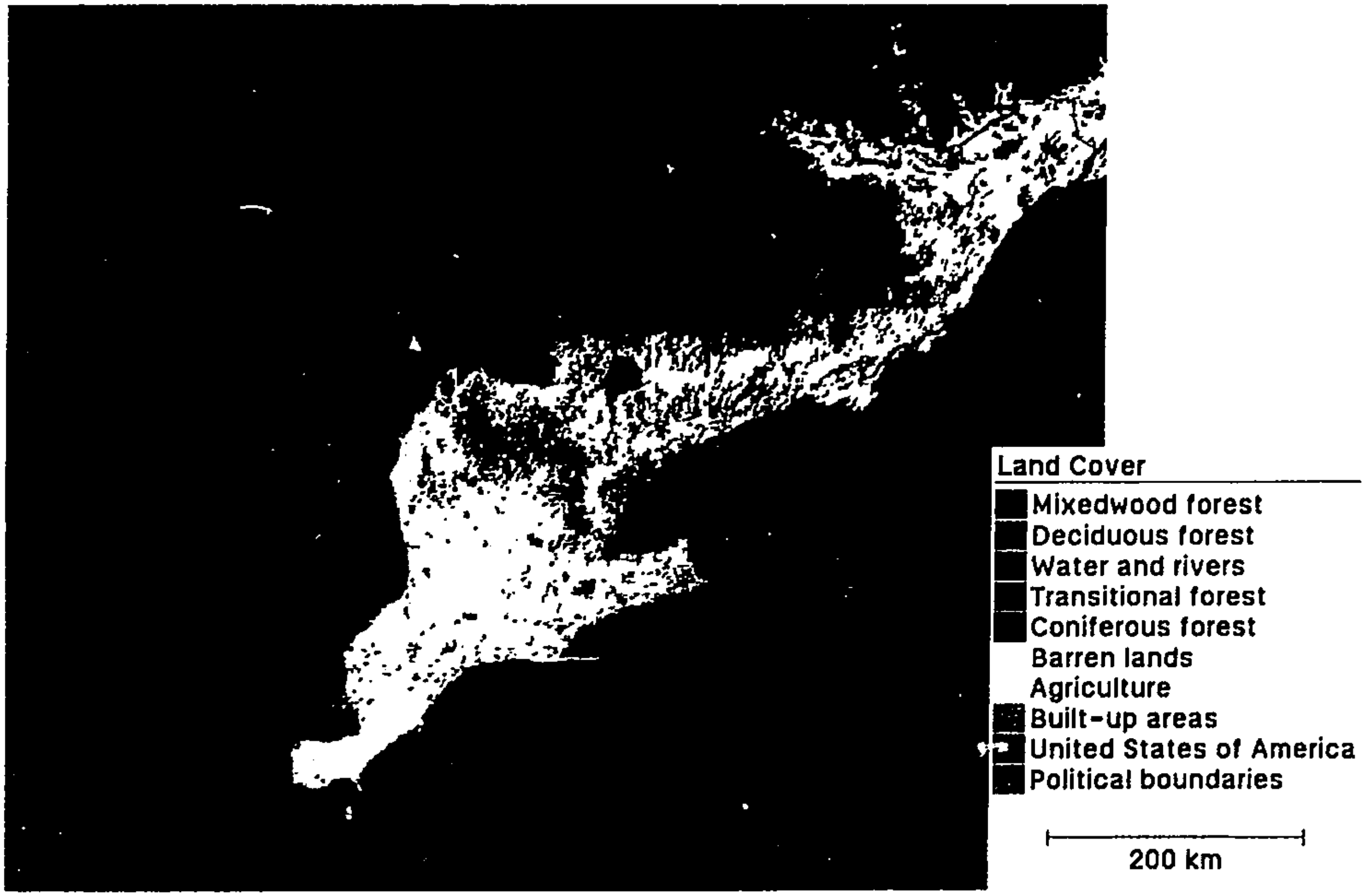
a pixel resolution of 1 km^2 and identified ten land cover classes: arctic tundra, transitional, hardwood, softwood and mixedwood forest, agricultural land, rangeland/pasture, water bodies, 'other' non-forested (barren land) and cultural (urban) features (Lowe *et al.* 1990) (Figure II-2). Tundra, rangeland and barren land did not occur within the study area. The amount of land covered by each of the classes listed above was totalled for each UTM square.

To give an indication of the degree to which the land cover over a UTM square was heterogeneous we calculated the number of forest classes per square, the number of different land cover classes and the Shannon-Wiener Index of diversity. The Shannon-Wiener Index takes into account both the number of cover classes and the relative abundance of those classes and is calculated using: $H' = -\sum_{i=1}^{N} p_i \log_2 p_i$, where p_i is the proportion of the total area of a square covered by the ith land cover class.

Climatic data were taken from the Canadian Climate Normals 1951-80 from the Canada Climate Centre. This data set provided detailed, long term climatic information and the geographical locations for 292 weather stations in Ontario. Not every climatic parameter examined (Table II-1) was measured at every station. The number of stations per parameter ranged from 224-292, with the exception of 'The Number of Days with Snow Cover over 5cm' which was recorded at 33 stations.

Climatic parameters were interpolated between measuring stations using a Voronoi mapping procedure, within a geographical information system (GIS). The result was a surface of polygons in which the climate at any given point was assumed to be the same

Figure II-2. Land cover over southern Ontario as classified from NOAA AVHRR-LAC satellite imagery.


Land Cover
Mixedwood forest
Deciduous forest
Water and rivers
Transitional forest
Coniferous forest
Barren lands
Agriculture
Built-up areas
United States of America
Political boundaries
200 km

as that of the nearest climate station. From these surfaces, average values for all of the climatic parameters were calculated for each of the UTM squares.

Human population, occupied dwellings and the geographical locations of 14 165 Enumeration Areas were obtained from the 1986 Canadian Census (Statistics Canada 1986). Human population and the number of occupied dwellings were each summed for each UTM square.

Locations and areas of protected areas were extracted from the National Conservation Areas Database (Environment Canada 1992). Parks were represented by points in their approximate geographical centres. Small parks were considered to be entirely within the UTM square of their index point. The five parks larger than 100km^2 were located directly on Canadian National Topographic Survey map sheets (1:50 000) and a planimeter was used to calculate their area in the appropriate UTM squares.

The geographical locations and extents of different soil types over southern Ontario were digitised from the North American sheet of the FAO (1970-1978) map of soils. The total concentrations of exchangeable bases, integrated over the top 100cm of the soil profile, were calculated from accompanying soil nutrient profiles (FAO 1970-1978). This estimate of soil fertility was then averaged within each of the UTM grid squares in southern Ontario.

GIS as a Data Management Tool

SPANS GIS (®TYDAC Technologies), a geographical information system (GIS), was used to digitally re-create the ABBO's scheme of UTM squares. This proved to be more difficult than anticipated because the richness data extend across three UTM zones. Re-creating the ABBO grid in a UTM projection-based SPANS study area ensured precise positioning of the gridlines using their UTM co-ordinates rather than conversion into latitude/ longitude for georeferencing. SPANS study areas based on UTM projections, cannot encompass more than one UTM zone.

We therefore created three study areas, one for each of UTM zones 16, 17 and 18 that cover southern Ontario. A grid was built in each study area and exported as vectors. The vectors were then imported into the main study area (based on a Lambert Conformal Conic Projection) and transformed into maps. The squares in each of the three maps were classified to reflect their UTM zone and co-ordinates. The three maps were then overlaid and the resulting map was edited to remove grid squares that were not included in the ABBO.

Environmental data were imported into SPANS GIS in order that they could be queried according to the 100 km^2 grid scheme for which we had avian species richness information. The values for the environmental variables occurring in a square were then either summed (park area, population, dwellings and land cover) or averaged (climate and soil fertility). Averages were calculated by weighting each observation according to the proportion of the UTM square to which it applies.

These calculations resulted in a matrix of 1721 UTM squares by 65 variables, in which each UTM square had associated values for the number of bird species, migrants etc. and the descriptors of the environment. These matrices were then exported to SYSTAT for graphical and statistical analysis.

Analysis

To test for relationships between species richness and the environmental variables, we first examined scatterplots of the relationships in order to assess the error structure and the functional form of the relationships. In order to stabilise the variance, several of the response variables were transformed (Chapters III and IV). These transformations resulted in normally distributed (Lillifors' test $p>0.05$) and homoscedastic (by visual inspection) residuals in most of the subsequent statistical models. The following predictor variables were also logarithmically transformed: human population, the number of occupied dwellings, and park area.

Trends in each of the richness - environment relationships were examined using LOWESS curves (Cleveland 1979) plotted in SYSTAT (®SYSTAT). Based on the shape of these curves, polynomial models, up to fourth order, were fitted to each of richness - environment relationships.

The polynomials were then combined into multiple regressions to statistically determine how much of the variation in richness could be related to the present set of predictor variables. Both multiple linear regressions (Appendix B) and multiple polynomial regressions (Appendix C) were constructed. Forward stepwise selection was used to determine the order of inclusion of predictors into the models. Individual predictors were added into the multiple polynomial regressions based on the combined F-value for all terms in the polynomial.

Concern over the dependent variables being counts, rather than continuous, and that the resulting error structure in our statistical models might be more appropriately approximated by Poisson distribution (rather than a normal distribution), led to further analysis of the data using generalised linear models (GLMs). In GENSTAT (®Lawes Agricultural Trust, Rothamsted Agricultural Station), GLMs for each of the measures of richness were calculated (specifying a Poisson error term and a log link function), with the environmental variables (restricted to first order) added into the model using forward selection. Very similar results were obtained for almost all the richness - environment models whether one used GLM or ordinary least squares regression (OLS). We therefore will concentrate on the results of OLS regressions in subsequent chapters. A comparison of results from both methodologies is presented in Appendix B.

The regression analysis detailed above was repeated using total avian species richness and the richness of the different life history guilds as response variables. Some of the measures of richness covaried strongly with observer effort (Chapters III and IV). However, removing the effect of observer hours (i.e. adjusting for observer hours as a polynomial covariate) could potentially obscure some of the relationships between richness and the environmental characteristics because observer hours was also correlated with many of the environmental variables investigated in this study (Table II-2). Therefore, we calculated all the richness - environment relationships both controlling for, and ignoring, the influence of observer hours. To remove the effects of sampling intensity, we examined partial correlations between richness and environmental variables, while holding the number of observer hours constant.

We also calculated the relationships between total avian species richness and the environmental characteristics controlling for the effects of temperature (i.e. adjusting for

Table II-2. Simple Pearson correlations among the environmental predictor variables discussed in the text. Although some of the relationships were detectably non-linear, polynomial relationships were only marginally stronger than the linear ones described here. All correlations were significant at $p<0.05$ (based on n-2 d.f.), except those denoted n.s. N=1721.

	Observer hours	Mean ann. temperature	Human pop.	Agricultural land	Total forest	Soil fertility
Observer hours	1.000					
Mean annual temperature	0.306	1.000				
Human population	0.355	0.590	1.000			
Agricultural land	0.198	0.670	0.597	1.000		
Total forest	-0.197	-0.767	-0.560	-0.798	1.000	
Soil fertility	0.108	0.525	0.411	0.553	-0.480	1.000
Park area	0.116	n.s.	n.s.	n.s.	n.s.	-0.078

mean annual temperature as a polynomial covariate). As with observer hours, we removed the effects of temperature by examining partial correlations between richness and environmental variables, while holding mean annual temperature constant.

CHAPTER III - TOTAL AVIAN SPECIES RICHNESS

Abstract

Habitat availability and energy are two aspects of the environment hypothesised to influence the number of species found in an area. The former has been shown to be important on smaller spatial scales, while energy has been associated with patterns of species richness at larger spatial scales. We tested the hypothesis that the number of breeding birds in 100km^2 squares over southern Ontario, Canada is related to aspects of climate, land cover, land cover heterogeneity, human impact and amount of protected area.

Temperature and total forest area were the strongest environmental correlates of avian richness. Even so, they each explained only slightly more than 10% of the variation in species numbers. Other environmental variables (e.g. soil fertility, parkland, human population) were significantly related to avian species richness over southern Ontario, but they explained negligible amounts of the variation in richness. We also found that examining the form of the richness-habitat relationships before adjusting for covariation with temperature could lead to errors in interpretation of the trends.

We conclude that at this spatial scale, neither of the two sets of hypotheses adequately describe the variation in avian species richness over southern Ontario to warrant further investigation of mechanistic links. Either the richness - environment relationships predicted by these two sets of hypotheses are surprisingly weak at this spatial scale, or the environmental data was not sufficient, in either scale or character, to address the hypotheses.

Introduction

The number of species in an area, or species richness, is arguably the most fundamental characteristic of ecosystems (MacArthur and Wilson 1967, Schluter and Ricklefs 1993). Obvious spatial patterns in species richness have led to much research on, and numerous hypotheses about, the causes of the variation observed. While debate about which factors control richness continues, concerns over decreases in species richness and possible effects on ecosystem function and productivity have become prominent (Wilson 1992, Huston 1994, Naeem *et al.* 1994, Ricklefs and Schluter 1993a, Sirica 1994, Tilman and Downing 1994).

Two quite disparate groups of hypotheses have been proposed to explain patterns of species richness. One group suggests that the number of species existing in an area is limited by energetic and historical constraints (Wright 1983, Ricklefs and Schluter 1993b). A second, strikingly different approach, suggests that the number of species in an area is regulated by habitat availability (Rosenzweig and Winakur 1966, Huston 1979, Lynch and Whigham 1984, Blake and Karr 1987).

The first group of hypotheses emphasises relationships between richness and factors thought to influence growth, reproduction and evolution of organisms. Available energy, energy capture, resource partitioning and evolutionary history are all thought to influence the flow of energy through a system and the number of species found therein. Brown (1981) suggests mechanisms by which the partitioning of available energy between individuals and species, as well as minimum energy requirements for species viability combine to determine the maximum number of species that can exist in an area.

Recent studies have suggested that productivity might integrate many aspects of the processes mentioned above, and that it could be one of the environmental regulators of species richness (Huston 1993, Rosenzweig and Abramsky 1993).

At large, continental scales, species richness in many different groups of organisms increases with climatic surrogates for productivity (Wright 1981, Currie and Paquin 1987, Adams and Woodward 1989, Wright *et al.* 1993, but see Latham and Ricklefs 1993). Specifically in the Aves, Currie (1991) found that about 70% of the variation in the number of bird species over North America can be statistically attributed to temperature-related variables such as solar radiation and potential evapotranspiration (PET). Several explanations of this phenomenon based on the partitioning of resources have been proposed (Hutchinson 1959, Brown 1981). Each species in an area requires a certain amount of energy, or production, to maintain a viable population of individuals in that area. Increased production leads to more species maintaining viable populations. Although the mechanism has been contested (Root 1988, Rohde 1992), species richness has almost always been observed to increase with productivity on large spatial scales.

At finer spatial scales, species richness has been related to other surrogates of productivity such as soil fertility (Huston 1993), accumulated plant biomass (Moore and Keddy 1989) or local precipitation (Abramsky and Rosenzweig 1984). At these scales, species richness usually shows peaked (increasing then decreasing) or negative relationships with these variables (Rosenzweig and Abramsky 1993). The bitonic productivity - richness relationships are consistent with Huston's (1979, 1994) hypothesis that rates of competitive displacement determine patterns of species richness.

Rosenzweig and Abramsky (1993) argue that the positive phase of the peaked relationships is due to higher productivities supporting larger populations of more species, while the decreasing phase could be the result of inter-taxon competition, a reduction in the covariance of competing population densities or reduced environmental heterogeneity.

The second group of hypotheses, those that link species richness to habitat availability, emphasise the requirements of individual species for particular types of habitat such as forest-interior, open fields, wetlands or seashore. Since many species are habitat-specific, areas that contain more habitat types, or larger areas of appropriate habitat, should have more species. Thus, patterns of species richness are generally thought to respond to the type, amount, complexity and pattern (in space and time) of habitats, or "habitat or niche diversity" (e.g. MacArthur *et al.* 1962, Arthur 1988). Habitat loss, both in terms of decreases in the overall amount, and changes in the character of the habitat (niche simplification), has been postulated as a main factor responsible for species' extirpations and extinctions (Saunders 1989, Ehrlich and Ehrlich 1992, but see Terborgh 1992). This hypothesis would predict that regional patterns of richness should be related to measures of what we will call "habitat availability": such as the area of undisturbed habitat and indices of habitat diversity.

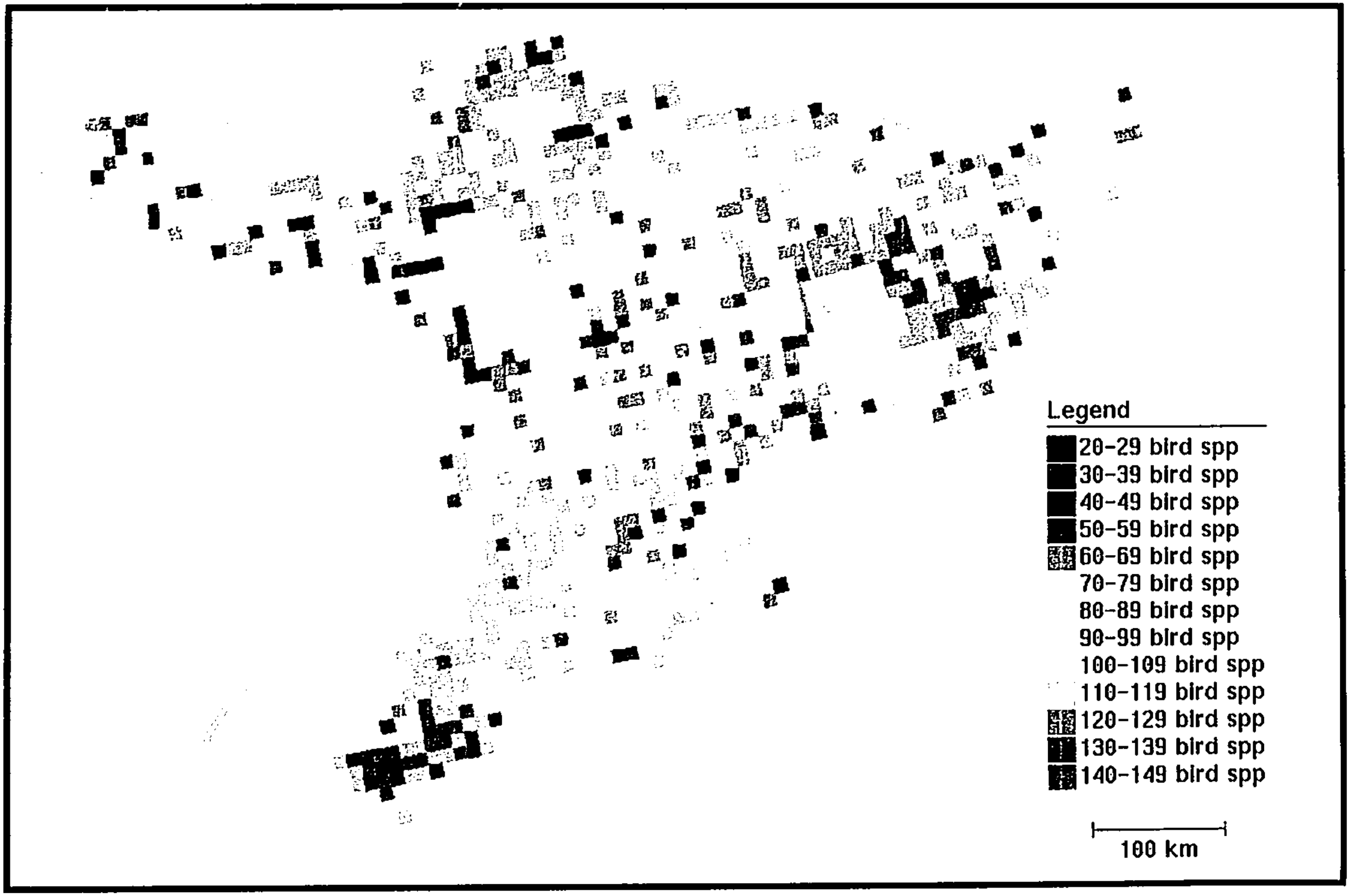
Relationships between habitat characteristics and avian species investigated on finer spatial scales (<1 000 km^2) invariably associate characteristics of the vegetation with habitat availability. Three characteristics of vegetation that are repeatedly linked with the species richness in an area are: the amount of forested area, vegetation composition and vegetation configuration (MacArthur and co-workers 1966 and references therein, Karr and Roth 1971, Whitcomb *et al.* 1981, James and Wamer 1982, Freemark and Merriam 1986). In general, more bird species are found in those areas with more forest and more complex forest.

In this study, we examined the species richness - environment relationships predicted by the energy and the habitat availability hypotheses using the variation in bird species richness in 100 km^2 squares over a 200 000 km^2 area in southern Ontario, Canada. The energy - richness hypothesis predicts that avian richness should be positively related to variables that affect primary productivity such as temperature, precipitation or soil fertility (Table II-1). The habitat availability hypotheses predict that bird species numbers should increase with increased habitat area. Unable to quantify habitat *per se*, at this spatial scale, we used remotely-sensed information on land cover as the best available surrogate. Specifically, we examined the relationships between the number of breeding bird species as related to: climate, land cover, land cover diversity, soil fertility, human population and the amount of parkland over southern Ontario (see Table II-1).

Methods

Bird distribution data were taken from The Atlas of the Breeding Birds of Ontario (ABBO) and were used to calculate species richness for 1721, 10 km by 10 km squares (UTM squares) over southern Ontario (Cadman *et al.* 1987, Figure III-1). These atlas data were assembled over five years using a network of birdwatchers that attempted to

Figure III-1. The spatial distribution of total avian species richness in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study.


Legend
20-29 bird spp
30-39 bird spp
40-49 bird spp
50-59 bird spp
60-69 bird spp
70-79 bird spp
80-89 bird spp
90-99 bird spp
100-109 bird spp
110-119 bird spp
120-129 bird spp
130-139 bird spp
140-149 bird spp
100 km

census thoroughly avian species' presence and absence over southern Ontario. The use of volunteers incurred certain inevitable errors which were mitigated by the Atlas committee as much as possible through independent verification of sightings and the recording of the number of observer hours per square.

Note that the data that comprise the ABBO are collected in a fundamentally different manner from, and with different goals than, those of the Breeding Bird Survey (BBS). The latter emphasises year-to-year variations in populations over time. The ABBO, in contrast, aimed for exhaustive censusing of all the species occurring in each UTM square. The latter method encouraging comparisons between squares over space.

Breeding bird observations were classified into 'confirmed breeding', 'probable breeding', 'possible breeding' and 'observed species' according to 17 criteria that assessed breeding evidence (Cadman *et al.* 1987). We used both the first two, and the first three classes of breeding evidence to compute two measures of avian richness. Correlations of these two indices of richness with the environmental variables were qualitatively similar. Since excluding 'possible' breeders significantly increased the covariation between richness and observer effort, the results with possible breeders included in the richness calculations are reported here. We rejected UTM squares with fewer than 10 hours of observer effort and condensed the remaining ABBO data into a presence/absence matrix of 232 species in 1721 squares. Most of these squares (N=1625) had 16 or more observer hours, the a priori goal of the atlassing committee (Cadman *et al.* 1987). The binary presence/absence matrix was used to calculate the avian species richness per UTM square and these numbers were related to characteristics of the environment described below.

Seven land cover classes (Table II-1) were identified for southern Ontario using NOAA AVHRR land cover satellite images interpreted by the Manitoba Centre for Remote Sensing (Lowe *et al.* 1990). These data were at a pixel resolution of 1km^2. The area of each land cover class in each UTM square was computed, along with the number of different land cover classes per square and the number of forest classes per square. As a measure of land cover heterogeneity, the diversity of land cover classes within each square was measured using the Shannon-Wiener Index of diversity: $H' = -\sum_{i=1}^{N} p_i \log_2 p_i$, where p_i is the proportion of the total area of a square covered by the ith land cover class.

Long term climate normals for almost 300 stations across southern Ontario were obtained from the Atmospheric Environment Service at the Canadian Climate Centre, Toronto, Canada. Not every climatic parameter (Table II-1) was measured at every station; consequently, the number of stations per climatic variable ranged from 224-292, with the exception of 'The Number of Days with Snow Cover over 5cm' which was recorded at 33 stations. The points were interpolated into a surface of polygons using a Voronoi mapping procedure in which the climate at any given point was assumed to be the same as that of the nearest climate station. From these surfaces, average values for all of the climatic parameters were calculated for each of the UTM squares.

The geographical locations and extents of different soil types over southern Ontario were digitised from the North American sheet of the FAO (1970-1978, 1:5 000 000) map of soils. The total concentration of exchangeable bases, integrated over the top 100cm of the soil profile, was calculated from accompanying soil nutrient profiles (FAO 1970-1978). This estimate of soil fertility (Huston 1993) was then averaged within each of the UTM grid squares.

Locations and areas of parks were extracted from the National Conservation Areas Database (Environment Canada 1992). Parks were represented by points in their approximate geographical centres. Small parks were assumed to be entirely within the UTM square of their index point. The five parks larger than 100 km^2 were located directly on Canadian National Topographic Survey maps (1:50 000). Total park area was then calculated for each UTM square.

Census statistics on human population and the number of occupied dwellings, for 14 165 enumeration areas, were extracted from the 1986 Canadian Census (Statistics Canada) and summed for the each of the UTM squares.

The spatial manipulation and querying of the data described above was done within SPANS GIS (©TYDAC Technologies Inc.) and resulted in a database referenced by UTM grid square, containing measures of richness and the environmental attributes. These values were then used in general linear models relating each of the environmental variables to avian species richness.

To test for relationships between species richness and the characteristics of the environment, we first examined scatterplots of the relationships smoothed with LOWESS curves (Cleveland 1979), in order to assess the error structure and the functional form of the relationships. Since the residuals were approximately homoscedastic, species richness was left untransformed. The following predictor variables were logarithmically transformed: human population, the number of occupied dwellings, and park area. Polynomial models, up to fourth degree, were then fitted to each of the richness - environment relationships.

Multiple polynomial regressions were calculated to determine how much of the variation in richness could be related to the present suite of predictor variables. Forward selection was used to determine which predictors to include in the models. Individual predictors were added into the multiple polynomial regressions based on the combined F-value for all terms in the polynomial.

Significance tests of the statistics were calculated assuming that each square contributes one degree of freedom to the analysis. If the error in our models is spatially autocorrelated, then squares actually contribute <1 degree of freedom. We do not explicitly address the potential problem of autocorrelation here. However, even if we conservatively assume that each quadrat contributes only 0.1 degrees of freedom, none of the qualitative conclusions presented below are altered.

Results

Avian species richness varied from 21 to 146 species in the 1721 UTM squares across southern Ontario. The central and eastern portions of the province tended to be species-rich, while the northern and south-western parts of the study area had fewer species of breeding birds (Figure III-1).

The variable most strongly related to species richness proved to be the number of observer hours ($R^2=0.23$, $p<0.001$). More bird species were found in squares in which people spent more time looking, despite the efforts of the ABBO co-ordinators. To remove the effects of sampling intensity, we examined partial correlations between richness and environmental variables, while holding the number of observer hours constant (i.e. adjusting for observer hours as a polynomial covariate). However, the number of observer hours is also correlated with many of the environmental variables investigated in this study (Table II-2). For example, human settlement in Ontario varies strongly with latitude. Southern parts of the province were both more densely settled and more thoroughly censused for birds than were remote areas. Removing the effect of observer hours could potentially obscure some of the relationships between richness and the environmental characteristics. We therefore report both simple relationships and relationships obtained after controlling for the number of observer hours. Statistically controlling the number of observer hours alters the form of the richness - environment relationships in some cases, but it does not change the relative strength of the relationships or the overall spatial patterns in avian species numbers (Table III-1).

Avian species richness was significantly related to almost all of the environmental variables in this study, with the most important of these listed in Table III-1. While significant, the relationships are not strong, and none of the predictors individually explain more than 13% of the variation in the number of bird species over southern Ontario.

Table III-1. Environmental characteristics most closely related to variation in avian species richness in 100 km^2 squares over southern Ontario, and selected other relationships discussed in the text. Many of the relationships are non-linear and they were, therefore, described by polynomial functions. For each relationship, the coefficients of determination adjusted to account for the number of terms in the polynomial are shown (R^2_{adj}). A representation of the general shape of the relationship is also given: peaked (⇗⇘), increasing (⇗) and decreasing (⇘). All relationships are significant at $p<0.001$ (and they remain significant at $p<0.05$ after correction for multiple comparisons). Non-significant relationships are denoted by n.s. N=1721.

Predictor variables	**Total avian species richness**		**Avian species richness controlled for observer hours**		**Avian species richness controlled for mean annual temperature**	
	R^2_{adj}	shape	R^2_{adj}	shape	R^2_{adj}	shape
Observer hours	0.229	⇗	---	--	0.251	⇗
Mean annual temp.	0.111	⇗⇘	0.114	⇗⇘	---	--
Total forested area	0.100	⇗⇘	0.131	⇗	0.113	⇗
Water area	0.086	⇗⇘	0.061	⇗⇘	0.104	⇗⇘
Agricultural land	0.073	⇗⇘	0.047	⇘	0.039	⇘
Heterogeneity	0.059	⇗	0.04	⇗	0.048	⇗
Human population	0.029	⇘	0.006	⇗	0.018	⇗
Park area	0.033	⇘	n.s.	--	0.012	⇘
Mean soil fertility	0.013	⇗⇘	0.009	⇗⇘	n.s.	--

The greatest amount of variation in avian richness was explained by measures of temperature. Mean annual temperature was the best correlate of avian species richness but only explained 11% of its variation (Table III-1). As a function of mean annual temperature, the number of bird species in 100 km^2 squares increased to a maximum near 6.0°C, and then decreased at higher temperatures (Figure III-2). This peaked relationship remained when observer hours were statistically held constant.

Since many of the remaining environmental variables that were related to richness also covaried somewhat with temperature (Table II-2), we considered both simple correlations and partial correlations controlling for temperature. Like observer hours, controlling for temperature altered the shape of some of the environment - richness relationships. The relative strengths of the correlations with species richness did not change.

Of the land cover variables, the number of bird species was most closely related to total forest area. Even so, total forest area accounted for only 10% of the variation in avian species numbers over southern Ontario. The relationship was peaked, with maximum numbers of species tending to occur when about 40%-50% of a UTM square was classified as forest (Figure III-3). Controlling for observer hours and temperature strengthened the relationships slightly and changed their shape. Richness increased monotonically with the amount of forest cover in a square when observer hours or temperature are statistically controlled (Figure III-4). Thus, fully forested squares had, on average, 13 more species than those with no forest.

Figure III-2. The relationship between total avian species richness and climate (temperature) in 100 km^2 UTM squares over southern Ontario, Canada. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).

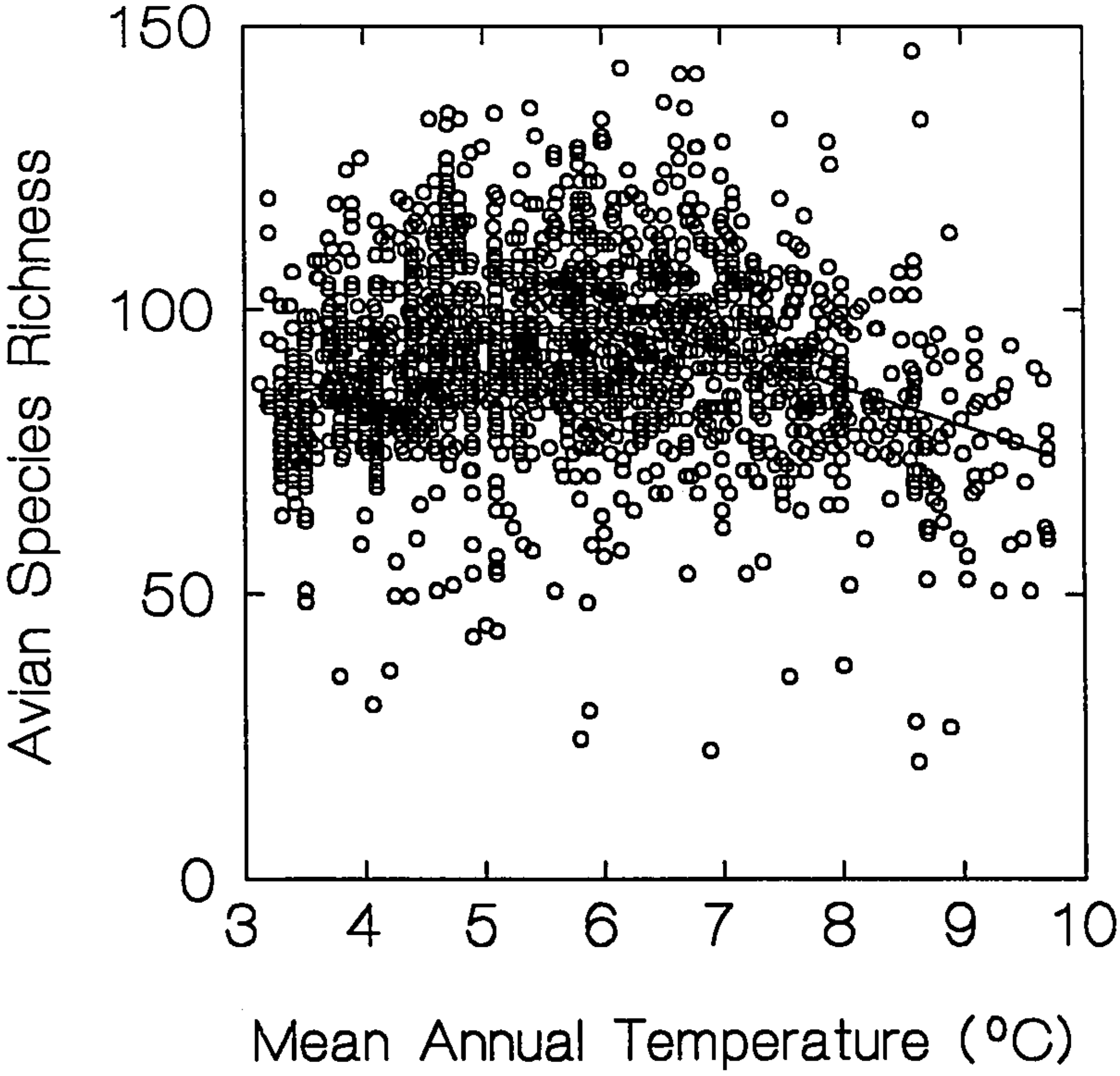

Avian Species Richness
150
100
50
0
3
4
5
6
7
8
9
10
Mean Annual Temperature (°C)

Figure III-3. The relationship between total avian species richness and the total amount of forested area in 100 km^2 UTM squares over southern Ontario, Canada. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).

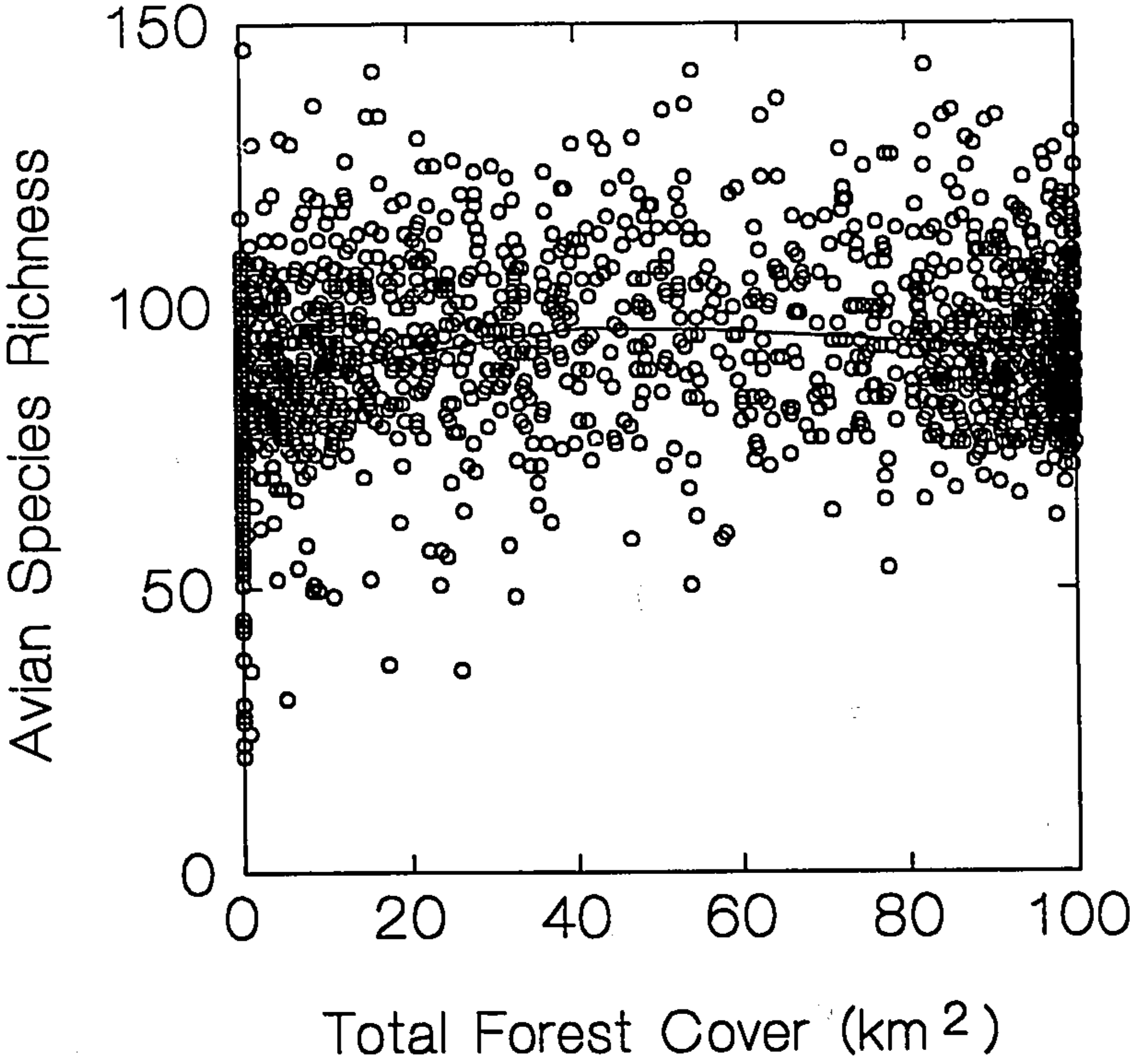
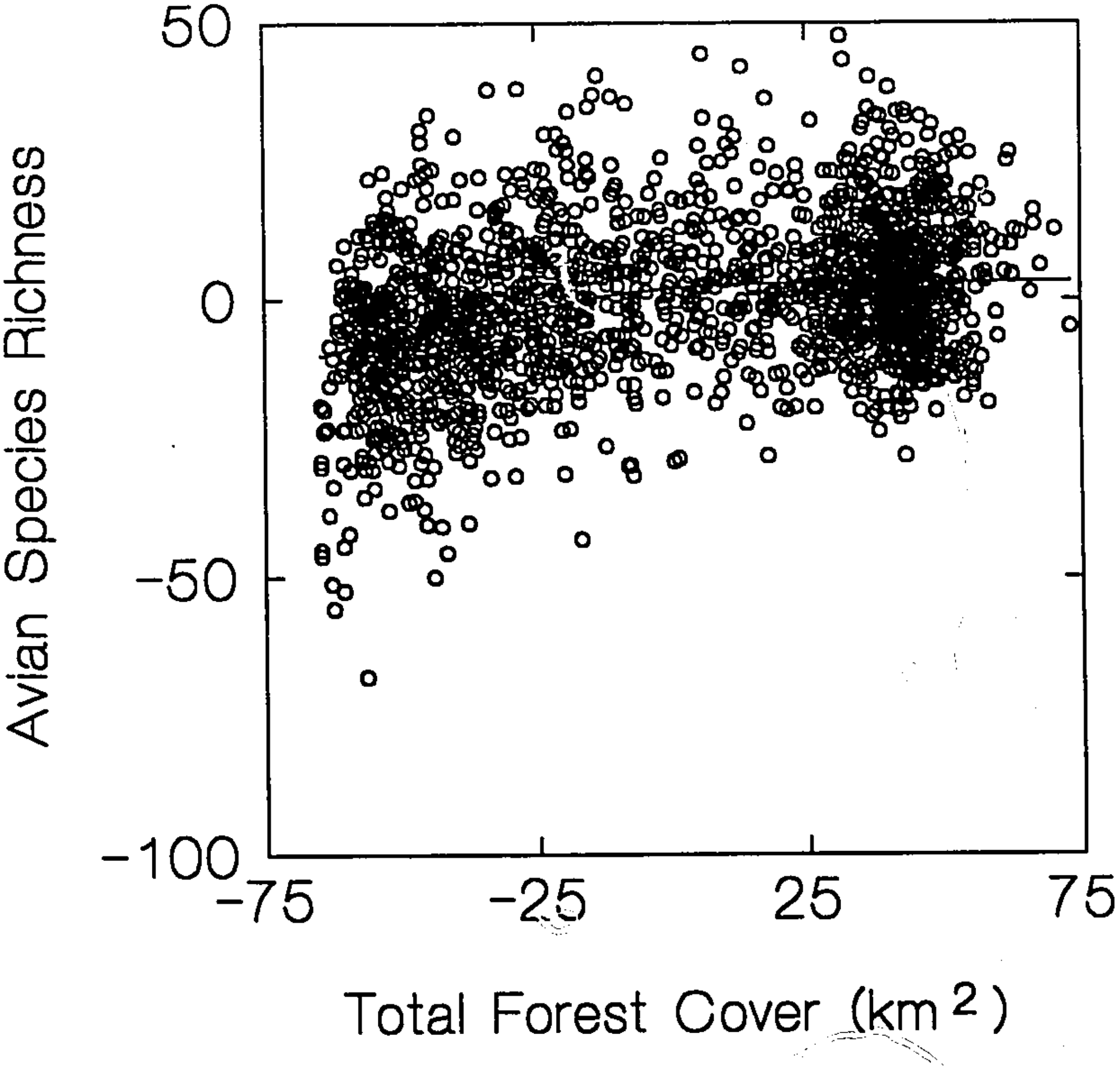

150
100
50
0
Avian Species Richness
0
20
40
60
80
100
Total Forest Cover (km 2)

Figure III-4. The relationship between total avian species richness and the total amount of forested area in 100 km^2 UTM squares over southern Ontario, Canada, after statistically controlling for the effects of observer hours (i.e. adjusting for observer hours as a polynomial covariate). The units on the this graph are not absolute. Rather, the units on the ordinate represent the difference between the observed species richness in a square and the expected number, given the observer effort. Similarly, the abscissa represents the difference between the observed amount of forest cover in a square and the average area of forest in quadrats having comparable observer effort. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).


50
0
-50
-100
-75
-25
25
75
Avian Species Richness
Total Forest Cover (km²)

Avian species richness was also relatively strongly related to agricultural land area (Table III-1). Richness was a peaked function of agriculture, suggesting that some agricultural land in the landscape mosaic may increase avian species richness (Figure III-5). However, agricultural area covaried strongly with temperature. Removing the effect of mean annual temperature revealed a monotonically decreasing relationship between richness and agriculture (Figure III-6). The rate at which bird species tended to be lost was especially high in those squares where more than fifty percent of their area was in agricultural production (Figure III-6).

Since forest cover, agriculture and temperature predictors are all correlated (Table II-2), we attempted to partition the variance attributable to each by statistically controlling for each of them in turn and re-computing their partial correlations with species richness. Just over 1% of the variation in richness could be attributed specifically to agriculture exclusive of the effects of the other two variables, while temperature accounted for 8%, and forest 9% of the variation in richness when the effects of the other two predictors were removed. While all three variables had independent, detectable effects on avian species richness, the effect of agriculture is mostly tied to the other two: forested areas have little agriculture and warm areas have more. Forest cover and temperature, in contrast, have strong independent links to the number of birds found in an area.

Avian species richness also increased with the diversity of land cover types (Shannon-Wiener index). While relatively little of the residual variation in the number of bird species was explained by this index of land cover diversity (Table III-1), there is a

Figure III-5. The relationship between avian species richness and the amount of agricultural land in 100 km^2 UTM squares over southern Ontario, Canada. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).

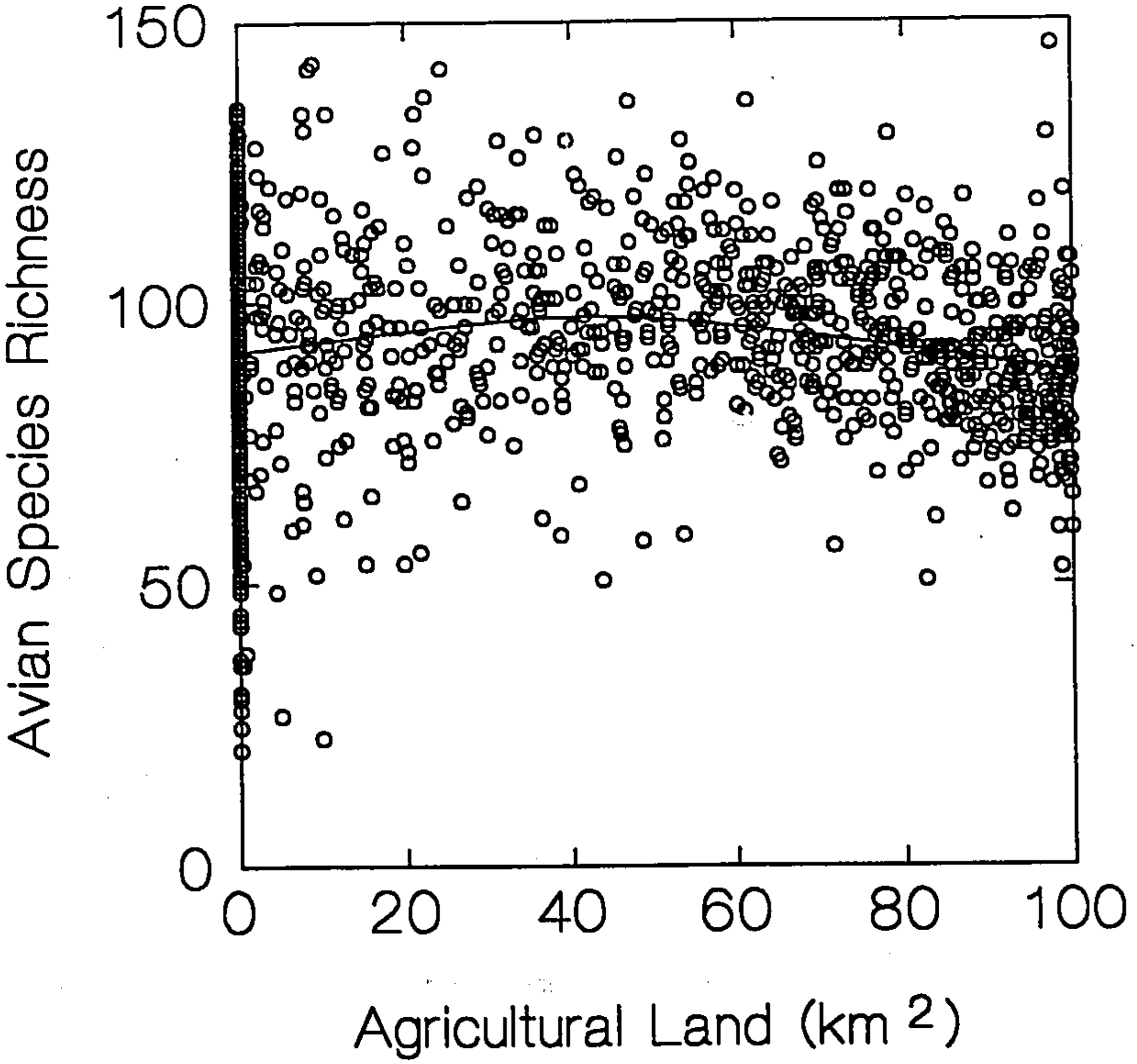
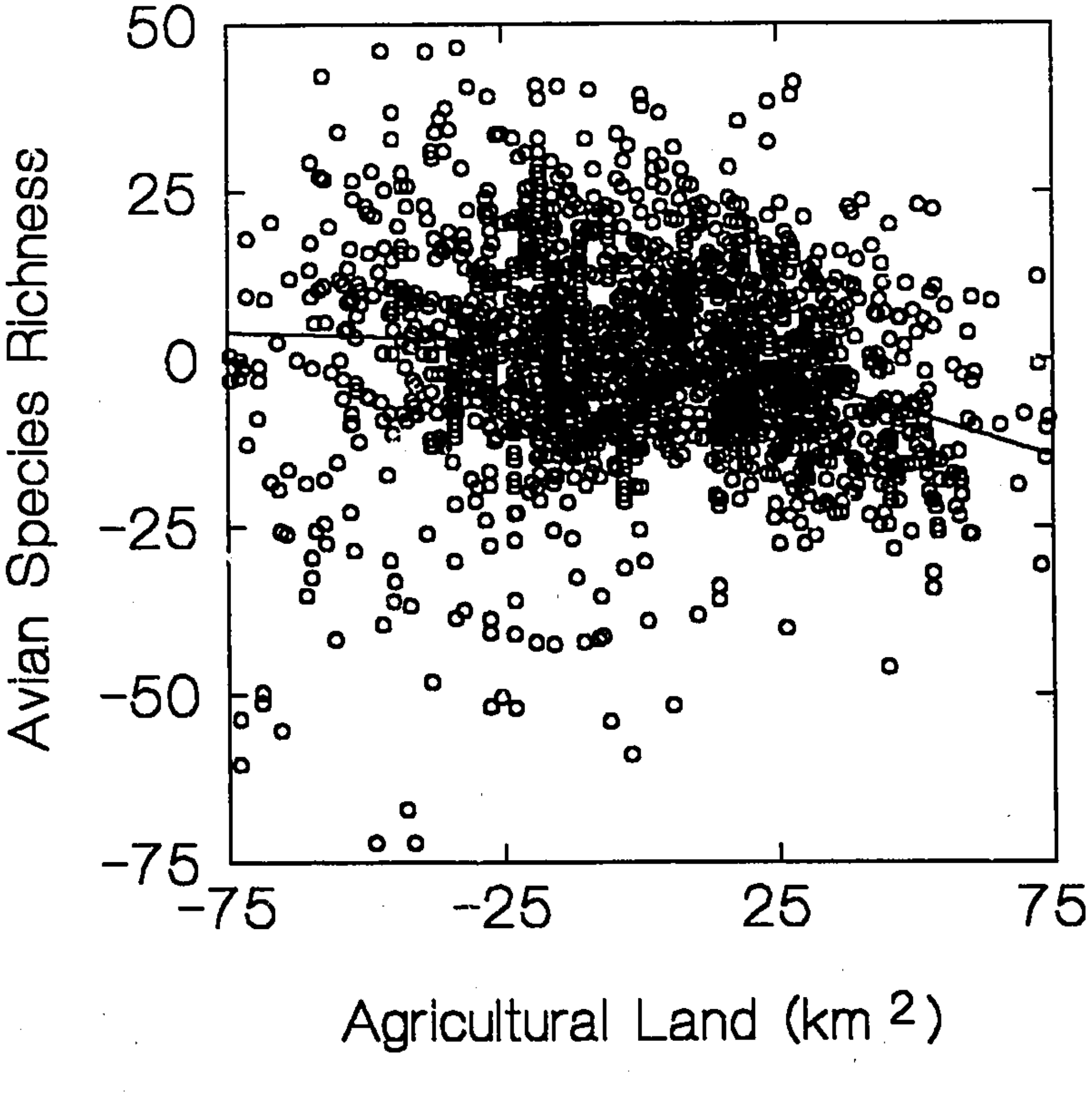

150
100
50
0
Avian Species Richness
0
20
40
60
80
100
Agricultural Land (km 2)

Figure III-6. The relationship between total avian species richness and agricultural land in 100 km^2 UTM squares over southern Ontario, Canada, after statistically controlling for the effects of mean annual temperature (i.e. adjusting for temperature as a polynomial covariate). The units on the this graph are not absolute. Rather, the units on the ordinate represent the difference between the observed species richness in a square and the expected number, given the temperature in that square. Similarly, the abscissa represents the difference between the observed amount of agricultural land in a square and the average amount of agricultural land in quadrats having comparable mean annual temperatures. A LOWESS curve, calculating locally weighted regressions (tension=0.7), was plotted to represent the general trend in the data (Cleveland 1979).


50
25
0
-25
-50
-75
-75
-25
25
75
Avian Species Richness
Agricultural Land (km 2)

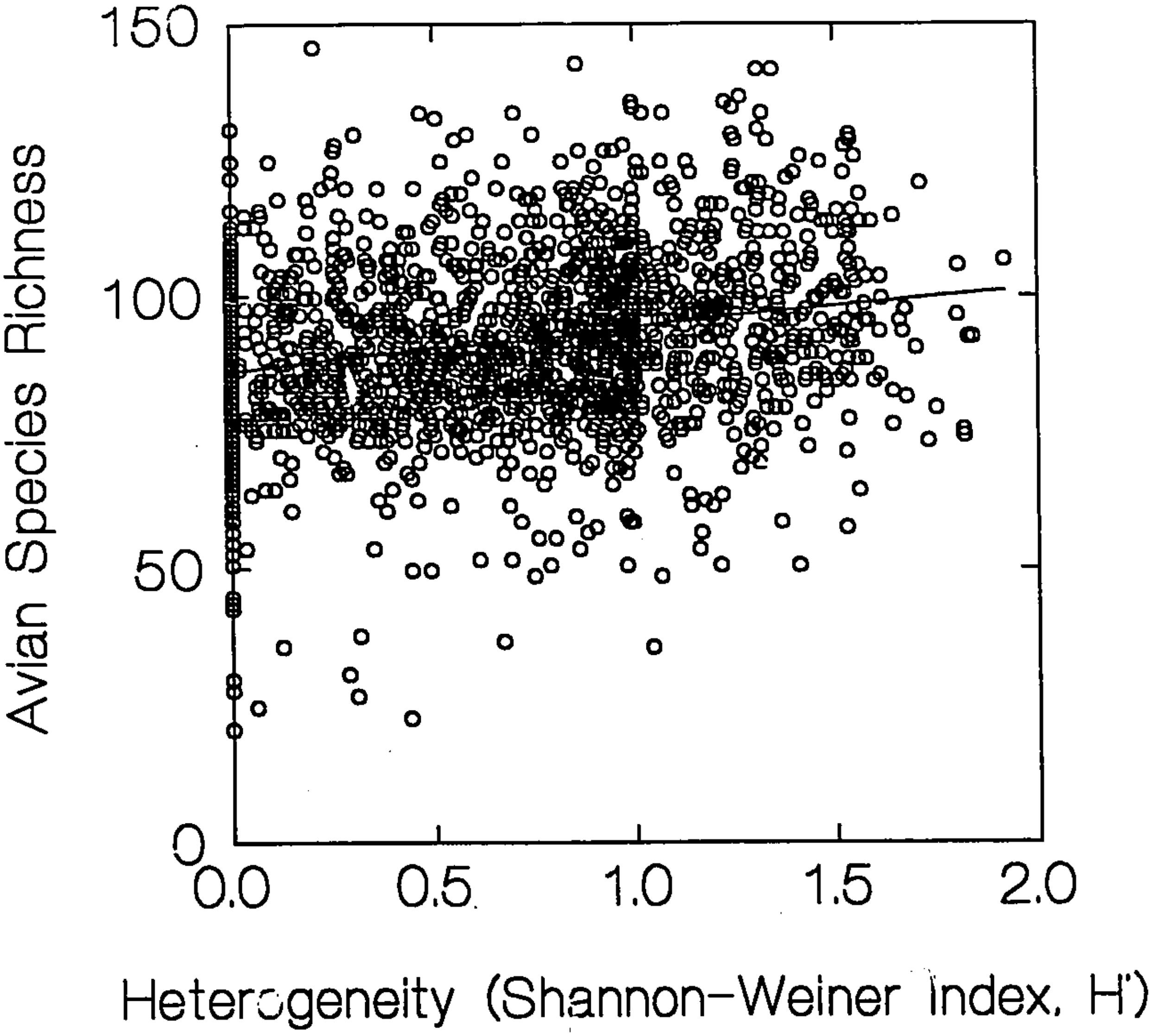
general increase in the number of species in an area with an increase in the diversity of habitats. Our measure of heterogeneity appears to be independent of both observer hours and temperature since controlling for either did not appreciatively change the form of the relationship or the amount of variation in richness explained (Table III-1, Figure III-7).

The amount of water in a UTM square accounted for almost 9% of the variation in avian species richness over southern Ontario (Table III-1). The relationships were peaked with maximum richness found in those squares with about 10 km^2 of water. Some surface water in a UTM square adds shore and water birds to the species list, but richness declines quickly thereafter as increased water area meant less land habitat available for terrestrial species.

Soil fertility, human population and park area each explained less than 4% of the variation in the number of bird species. These predictors also tended to covary strongly with temperature and observer hours and explained very little of the variation in avian richness once the latter were taken into account (Tables II-2 and III-1).

Multiple regressions explained between 30% and 45% of the variation in total avian species richness over southern Ontario. A multiple linear regression incorporating the environmental characteristics listed in Table III-1 explained 45% of the variation in the number of bird species over southern Ontario (30% if observer hours is excluded). All of the variables in Table III-1 were significant in these regressions except park area and soil fertility. When observer hours and temperature were statistically controlled, 24% and 37% of the variation in richness was explained by the remaining variables,

Figure III-7. The relationship between total avian species richness and the diversity of land cover classes, in 100 km^2 UTM squares over southern Ontario, Canada. The Shannon-Wiener index of diversity (H') represents a measure of both the number of land cover classes and their relative abudances per UTM square (see Methods). A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).


150
100
50
0
0.0
0.5
1.0
1.5
2.0
Avian Species Richness
Heterogeneity (Shannon-Weiner Index, H')

respectively. A polynomial regression including the five most strongly related predictor variables accounted for 39% of the variation in avian richness (Appendix C).

Discussion

We set out to test for relationships between avian species richness and various environmental characteristics linked to energy and habitat availability (as estimated by land cover). The energy - richness literature predicts strong links between species richness and factors related to productivity, while the habitat availability hypotheses suggest that associations with habitat amount, type and configuration should predominate.

Climatic factors, especially variables related to temperature, and soil fertility are two environmental factors thought to influence energy availability and primary productivity at temperate latitudes (Rosenzweig 1968, Huston 1993). If the variation in avian species richness, over southern Ontario, is the result of varying energy availability or primary productivity, then one should observe strong relationships between richness and these factors. At this spatial scale, the relationships between richness and climate are weak and those between richness and soil fertility are nearly non-existant. The latter, especially, contrasts with the suggestion that unproductive areas are most important for conservation because of their high species richness (Moore *et al.* 1989, Huston 1993). While this may be true for plants, the generalization apparently does not extend to birds at these smaller spatial scales.

Mean annual temperature was nonetheless the strongest correlate of avian species richness over southern Ontario. Even so, it only accounted for 11% (out of a 30% total) of the variance in richness explained by the environmental characteristics (11% out of a total 24% if observer hours are controlled). While mean annual temperature and energy availability might influence the number of bird species found over southern Ontario to some extent, it is unlikely that it is the prime cause behind the patterns observed.

After identifying the climate - richness relationships, we verified that they were neither an artefact of the interpolation procedure (see Methods) nor a carry-over effect of large-scale macroclimate. To confirm that the Voronoi mapping procedure did not create pattern, we re-calculated the climate - richness relationships using only those squares containing weather stations. The non-interpolated climate data were similarly related to avian species richness, but with less of the variation in avian richness explained (N<300 rather than 1721).

At the spatial scale of our study, part of the effect of temperature appears to reflect macroclimatic influences, and part reflects local temperature variation. To examine this, we re-calculated average temperatures for the ABBO squares based on gross, large-scale temperature information (2.5° by 2.5° quadrats, each about 50 000 km^2). Macroclimate (i.e. the climate averaged over 2.5° by 2.5° quadrats) explains about 5% of the variation in avian species richness over southern Ontario ($N=1721$, $p<0.001$), and has a significant effect even after controlling for local temperature ($N=1721$, $p<0.001$). Microclimate (i.e. climate in 10 km^2 squares) explains more (8%) of the variation in bird species numbers attributable to climate at this scale. The small amounts of variation in richness attributable to climate at this scale, contrast with results at larger spatial scales (Currie 1991) and suggest that while energy availability may be related to the size of the regional species pool, it is unlikely to determine the number of avian species found locally.

Is it possible, then, that the variation in avian species richness over southern Ontario is due varying habitat availability? The land cover variable most strongly related to avian species richness over southern Ontario was total forest cover. Like temperature, the total amount of forest in a UTM square accounted for small amounts of variation in species richness: 10% of the 30% total variance explained by the environmental predictors, or 13% of a total 24% when observer hours are controlled (Table III-1). Avian species richness increases with the amount of forest cover, indicating that areas with more relatively large patches of forest (i.e. those resolvable by the AVHRR satellite imagery) generally have more bird species. Information about the land cover at this resolution, while statistically significant, also provides relatively little information about the number of bird species found in 100 km^2 squares over southern Ontario.

This observation is consistent with several possible interpretations. The simplest is that avian species richness does not respond to the habitat characteristics (i.e. land cover) we measured. Either avian species richness could be quite insensitive to aspects of the land cover and vegetation at intermediate spatial scales (Wiens *et al.* 1987), or it might be related to environmental characteristics that we did not examine, such as habitat patch size, forest interior/edge ratios, wetland area and habitat configuration.

Alternatively, species richness could be responding to patch sizes and habitat cues at either larger or smaller scales than those examined here. At larger scales, distances to very large patches of suitable habitat (possible metapopulation 'sources') could be important (Pulliam 1988, Villard *et al.* 1989), while at much finer scales, the species composition and complexity of the vegetation cover might influence the number of species in an area (e.g. MacArthur *et al.* 1966). The 1 km^2 pixels of 'forest' in the NOAA AVHRR imagery included any 1 km^2 area with at least 50% forest canopy and often included grassland, marsh, bog and fen habitats (Lowe *et al.* 1990). If strong avian richness - habitat availability links exist at this spatial scale, the AVHRR imagery does not provide us with adequate information to identify those areas with more bird species over southern Ontario.

It is also possible that richness - habitat relationships are weak because the species that make up the species pool in this study respond to habitat characteristics in radically different ways, such that richness as a whole does not respond consistently to the variables representing habitat availability. Relationships between the richness of avian life-history guilds and environment characteristics will be examined in Chapter IV.

The weak richness - forest cover relationship is in striking contrast to the contention, much cited in overviews of environmental problems (Goudie 1986, Wilson 1992, Owen and Chiras 1995), that habitat loss and alteration is the prime cause of species loss. This is certainly true at the scale of the biosphere, where elimination of a species' habitat and its extinction cause a decrease in global species richness. However, at regional scales, our work with avian species richness suggests that habitat availability at this spatial scale has relatively little relation to the total number of species found in an area.

The weak effect of human activity on patterns of avian species richness, at this spatial scale, is also evident from the very weak relationships between richness and park area or human population. The former was chosen as an indication of the amount of relatively natural areas in a UTM square, while the latter represented, at least, a correlate of human impact. Neither of these predictors proved to have any relationship with the number of bird species found in an area. Surprisingly, species richness was not systematically higher in grid squares with parkland. However, if one examines only those squares with <25% forest, where parkland likely represents any remaining natural vegetation, there is a stronger positive relationship between richness and park area ($R^2=0.207$, $N=640$, $p<0.00005$). Weak richness-parkland relationships are nonetheless consistent with Kerr and Currie's (1995) observation at global scales that countries with greater amounts of protected land do not have lower frequencies of endangered bird species.

To conclude, the present study is the most extensive study of habitat - richness relationships at this spatial scale of which we are aware. It showed that mean annual temperature and the amount of forest cover are the best correlates of the number of bird species found in 100 km^2 squares over southern Ontario. However, each of these predictors independently explains only 8-13% of the variation in avian richness at this spatial scale. Neither the habitat availability variables, nor the surrogates for productivity explain enough of the spatial variability in avian species richness over southern Ontario for us to suggest that they might control patterns observed in the number of breeding bird species observed. Surrogates for both human impact (population) and lack thereof (parkland) explained almost none of the variation in avian richness at this scale. Other unidentified factors, or factors acting at other spatial scales, presumably account for the remaining variability in avian species richness.

Acknowledgements

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CHAPTER IV - AVIAN LIFE-HISTORY GUILD RICHNESS

Abstract

Many environmental factors have been suggested as possible influences on avian species richness. At intermediate spatial scales (quadrats 10^0 - 10^3 km^2 in size, over regions of 10^3 - 10^6 km^2) the relationships between total richness and environmental characteristics area relatively weak (Chapter III).

One possible explanation for these weak relationships is that different bird species can react very differently to similar aspects of the environment, such that total richness, as a whole, does not relate to any particular environmental variable. We grouped the breeding bird species found over southern Ontario, Canada by life-history traits and examined the relationships between the variation in richness of these groups (guild richness) and a suite of environmental variables that included, climate, human population, land cover, a land cover heterogeneity index, soil fertility and parkland.

Up to four times as much of the variation in guild richness can be explained by single environmental predictors compared to total avian species richness. The amount of variation explained depends on the life-history guild chosen, with conifer nesters and building nesters much more strongly related to environmental characteristics than other nesting guilds, and guilds based on migratory strategy.

The variation in richness of coniferous nesters and long distance migrants was most strongly related to total forest cover. Building nesters were strongly related to human population and the number of occupied dwellings. The richness of the other life-history guilds, like total avian species richness, were most closely related to measures of

temperature. We propose that the consistent effect of temperature on all the measures of richness represented a larger-scale influence of temperature (perhaps energy) on the regional species pool.

Guild richness rather than total avian species richness appears to be a more appropriate metric for conservation planners and managers at intermediate spatial scales. The guilds that are of interest are those that exhibit strong richness - habitat relationships. Further investigation of which life-history traits are appropriate for guild definition, and the specific habitat types associated with the richness of these guilds is suggested.

Introduction

The number of species in an area, or species richness, varies markedly through space. A great deal of research has focused on describing the variation of species richness across the biosphere and hypothesising why the patterns exist as they do. Yet, answering the question "why are there more species in some places than in others" remains one of the pre-eminent problems in ecology (May 1986).

A number of hypotheses have been proposed to explain the variation in species richness. They postulate that richness can be affected by: climate, climatic variability, history, habitat heterogeneity, soil fertility, energy, competition, predation, disturbance and other factors (reviewed in Currie 1991, Rodhe 1992, Ricklefs and Schluter 1993a, Huston 1994). There is evidence that most of these factors do indeed influence the number of species in an area, at least to some extent, on some spatial scales (Begon *et al.* 1990). Since most hypotheses predict that species richness is related to particular characteristics of the environment, we can begin to isolate which of these factors might be the most important causal determinants of richness by eliminating those that are not correlated with the variation in richness observed.

On large scales (quadrats 10^4 - 10^5 km^2 in size, extending over continents), species richness in many taxonomic groups increases with surrogates for energy availability like climate (temperature, evapotranspiration) and soil fertility (Wright 1981, Currie and Paquin 1987, Gentry and Emmons 1987, Adams and Woodward 1989, Huston 1993, Wright *et al.* 1993). Specifically in the Aves, Currie (1991) found that about 70% of the variation in the number of bird species over North America can be statistically attributed to environmental characteristics related to temperature.

In contrast, the number of bird species on local scales (quadrats 10^{-2} - 10^{0} km^2 in size extending over 10^{0} - 10^{3} km^2 areas) has been consistently related to habitat availability variables. Those local scale studies that have found strong richness - habitat relationships have tended to examine the species richness of particular groups of similar species, or "guilds" (Root 1967), rather than total avian species richness (e.g. Blake and Karr 1987, Gutzwiller and Anderson 1987). Habitat requirements, and thus what constitutes "available habitat", can differ greatly among species or groups of species (e.g. Noon *et al.* 1980, Cody 1985), and could potentially weaken relationships between total avian species richness and a particular habitat type. Nonetheless, the richness of many different groups of birds has consistently been related to aspects of plant cover, specifically the amount, structure, pattern and type of vegetation (e.g. MacArthur and MacArthur 1961, Roth 1976, James and Warner 1982, Wiens *et al.* 1987, Braithwaite *et al.* 1989, Urban and Smith 1989). Across eastern North America, up to 90% of the variation in richness in guilds like forest-interior and neo-tropical migrant birds, has been related to simply the amount of forest in an area (e.g. Galli *et al.* 1976, Whitcomb *et al.* 1981, Ambuel and Temple 1983, Schmiegelow and Nudds 1987, Villard *et al.* 1989).

At intermediate spatial scales (quadrats 10^{0} - 10^{3} km^2 in size extending over regions of 10^{3} - 10^{6} km^2), the relationships are much less clear. At these scales, total avian species richness is related to both habitat and energy availability (Chapter III). However, these relationships are considerably weaker than those observed at either local or continental scales, with just over 10% of the variation in avian species richness explained by either total forest cover or mean annual temperature in 100 km^2 squares over southern Ontario, Canada (Chapter III). The richness - environment relationships of North American shrubsteppe birds showed similar scale-dependence, with large-scale relationships becoming insignificant at intermediate spatial scales (Wiens *et al.* 1987).

It is conceivable that weakness of the intermediate scale total species richness - environment relationships is due to different species reacting inconsistently to particular environmental characteristics. At smaller spatial scales, there are definable guilds, whose variation in richness is related to particular aspects of habitat availability (e.g. Lynch and Whigham 1984, Blake and Karr 1987). Do similar groupings exist at intermediate spatial scales?

It is at intermediate spatial scales that richness - environment relationships are of particular importance, because it is at these scales that many civil administrative units (counties, townships and regional municipalities) make conservation and management decisions. It is important to identify what sorts of changes to the physical environment result in changes in richness. This information can then be incorporated into decisions regarding land zoning, parkland and infrastructure, all of which can influence the types, amounts and patterns of land cover and, potentially, species richness.

Partitioning total avian species richness into its guild components could be useful for conservation planning inasmuch as different values and conservation priorities are often accorded to different groups of species based on their taxonomy or life-history. Identifying the areas that are speciose for guilds of particular interest, as well as the environmental characteristics associated with these patterns, could be of special interest to conservation and park planners.

In order to test whether the species richness of different bird guilds relate differently to habitat characteristics, each of the bird species observed breeding in southern Ontario was classified by migratory strategy and nesting habitat. The richness of these guilds was then related to several environmental characteristics that represent some of the factors that have been hypothesised to influence richness. Specifically, we tested the hypotheses that the number of bird species in life-history guilds in 100 km^2 squares over 200 000 km^2 of southern Ontario is related to climate, land cover type, land cover heterogeneity, soil fertility, human population, and parkland.

Methods

Bird distribution data for 1721 UTM squares (10 km by 10 km) over southern Ontario were taken from The Atlas of the Breeding Birds of Ontario (ABBO) (Cadman *et al.* 1987). These atlas data were assembled over five years using a network of birdwatchers that attempted to census thoroughly avian species' presence and absence over southern Ontario. The use of volunteers incurred certain inevitable errors which were mitigated by the Atlas committee as much as possible through independent verification of sightings and the recording of the number of observer hours per square. These data were collected in a fundamentally different manner from, and with different goals than, those of the Breeding Bird Survey (BBS). Rather than emphasising year-to-year variations in populations over time, the ABBO aimed for exhaustive censusing of all the species occurring in each UTM square. The latter methodology encourages comparisons between squares over space.

Breeding bird observations were classified into 'confirmed breeding', 'probable breeding', 'possible breeding' and 'observed species' according to 17 criteria that assessed breeding evidence (Cadman *et al.* 1987). In this study we used species observations fulfilling the criteria for the first three classes of breeding evidence to compute guild richness. Initially, to be more conservative, we excluded 'possible breeders' from the richness calculations. However, we found that proportionally more 'possible breeding' species were observed in those UTM squares that had less observer effort. Lightly-censused squares, tended to be more remote and likely had more 'possible breeders' because additional breeding evidence was often not obtainable due to either time or physical constraints (D Hussell, Canadian Wildlife Service, personal communication). Therefore, to minimise the covariation between guild richness and the number of observer hours per square, we included 'possible breeders' in the guild richness calculations (Chapter III). We rejected UTM squares with fewer than 10 hours of observer effort. We then condensed the remaining ABBO data into a presence/absence matrix of 231 species in 1721 squares. Most of these squares (N=1625) had 16 or more observer hours, the *a priori* goal of the atlassing committee (Cadman *et al.* 1987).

The 231 bird species were assigned to 8 guilds (based on Ehrlich *et al.* 1988, Farrand 1983, Gauthreux, unpublished) (Appendix A). Each guild contained 9 to 146 species, and richness varied between 0 to 95 species per UTM square, per guild (Table IV-1). Species were classed as either long-distance migrants, (wintering south of

Table IV-1. The number of bird species (Total) included in life-history guilds based on nesting preference and migratory strategy, as well as the mean, standard deviation (S.D.), minimum (Min), maximum (Max) of the richness of those guilds in 100 km^2 UTM squares over southern Ontario, Canada. Also included are the power transformations (guild richness)^K used to stabilise the variance in the richness data for each guild. A total of 231 bird species were identified in 1721 squares.

Life-history Guild	Total	Mean	S. D.	Min	Max	K
Nesting habitat:						
Snag	29	13.2	2.7	1	21	1.5
Coniferous nesting	75	29.7	8.7	2	53	1.0
Deciduous nesting	84	41.3	7.1	7	62	1.0
Shrub nesting	55	24.7	4.0	5	38	2.7
Ground nesting	123	39.7	9.4	7	75	1.0
Building nesting	9	5.5	1.8	0	9	-*
Migratory strategy:						
Residents/short distance migrants	146	57.1	10.4	16	95	0.85
Long distance migrants	85	34.8	6.7	4	54	1.3

* no transformations were found that would satisfactorily stabilise the variance.

the Gulf of Mexico) or as residents/short-distance migrants. Nesting guilds were based on the types of habitat in which nests were commonly found. Each species was associated with one or more of the following nesting habitats: tree snags, coniferous forest, deciduous forest, shrubs (including grass), ground (including floating, cliffs and banks) and buildings (Ehrlich *et al.* 1988). The number of species in each guild (Table IV-1) was calculated for each UTM square. Guild richness was then related to characteristics of the environment described below.

Long term climate normals for almost 300 stations across southern Ontario were obtained from the Atmospheric Environment Service at the Canadian Climate Centre, Toronto, Canada. Variables related to temperature, precipitation and snow cover were all included in our analyses (Table II-1). Not every climatic parameter was measured at every station; consequently, the number of stations per climatic variable ranged from 224-292, with the exception of 'The Number of Days with Snow Cover over 5cm' which was recorded at 33 stations. The point observations were interpolated into a surface of polygons using a Voronoi mapping procedure in which the climate at any given point was assumed to be the same as that of the nearest climate station. From these surfaces, average values for all of the climatic parameters were calculated for each of the UTM squares.

The geographical locations and extents of different soil types over southern Ontario were digitised from the North American sheet of the FAO (1970-1978, 1:5 000 000) map of soils. The total concentration of exchangeable bases, integrated over the top 100cm of the soil profile, was calculated from accompanying soil nutrient profiles

(FAO 1970-1978). This estimate of soil fertility (Huston 1993) was then averaged within each of the UTM grid squares.

Seven land cover classes (Table II-1, Figure II-2) were identified for southern Ontario using NOAA AVHRR land cover satellite images interpreted by the Manitoba Centre for Remote Sensing (Lowe *et al.* 1990). These data were at a pixel resolution of 1 km^2. The area of each land cover class in each UTM square was computed, along with the number of different land cover classes per square and the number of forest classes per square. As a measure of land cover heterogeneity, the diversity of land cover classes within each square was measured using the Shannon-Wiener Index of Diversity : $H' = -\sum_{i=1}^{N} p_i \log_2 p_i$, where p_i is the proportion of the total area of a square covered by the ith land cover class.

Locations and areas of parks were extracted from the National Conservation Areas Database (Environment Canada 1992). Parks were represented by points in their approximate geographical centres. Small parks were assumed to be entirely within the UTM square of their index point. The five parks larger than 100 km^2 were located directly on Canadian National Topographic Survey maps (1:50 000). Total park area was then calculated for each UTM square.

Census statistics on human population and the number of occupied dwellings, for 14 165 enumeration areas, were extracted from the 1986 Canadian Census (Statistics Canada 1986) and summed for the each of the UTM squares.

The spatial manipulation and querying of the data described above was done within a geographical information system (SPANS GIS, ©TYDAC Technologies Inc.) and resulted in a database referenced by UTM grid square, containing measures of richness and the environmental attributes. These values were then used to relate guild species richness to each of the environmental characteristics.

While testing for relationships between guild richness and environmental characteristics, we examined the error structure and the functional form of the relationships. For several guilds, a power transformation was applied to improve the distribution of the residuals (Table IV-1). Regressions of transformed guild richness against the environmental characteristics then yielded homoscedastic, symmetrically distributed residuals for all guilds, except in the case of building nesters. The richness of building nesters only varied between 0-9 species, and we were unable to statistically transform it to stabilise the variance satisfactorily. Since the building nester richness data do not satisfy the assumptions of ordinary least squares regression, the results of these regressions should be interpreted with caution. In addition, the following predictor variables were logarithmically transformed: human population, the number of occupied dwellings, and park area. Polynomial models, up to third degree, were then fitted to each of the guild richness - environment relationships.

To determine how much of the variation in richness in each guild could be related to the environmental predictors, the guild richness-environment polynomials were then combined into a multiple polynomial regression for each guild. Individual predictors were added to the regression models through forward selection, based on the combined F-values of all the terms in the polynomial. Inclusion of a predictor, meant all the terms associated with that polynomial were added into the multiple regression.

Even after including 'possible breeders', guild richness was related to observer effort in our data set. In order to remove the effects of sampling intensity, we generated partial correlations between the richness of each guild and the environmental variables, while holding the number of observer hours constant (i.e. adjusting for observer hours as a polynomial covariate). However, the number of observer hours is also correlated with many of the environmental characteristics investigated in this study (Table II-2). Removing the effect of observer hours could potentially obscure some of the relationships between guild richness and the environmental characteristics. We therefore report both simple relationships and relationships obtained after controlling for the number of observer hours.

Results

There were three general spatial patterns of guild richness over southern Ontario. The most common spatial pattern (residents/short distance migrants, long distance migrants, deciduous nesters, ground nesters, shrub nesters and snag nesters) resembled that of total avian species richness and was characterised by a general decrease in richness towards the north and south-west, and a particularly speciose group of squares in the eastern part of the study area (Figures III-1, IV-1). In contrast, building nesters were most conspicuously species-rich areas along the southern edge of the study area (Figure IV-2). Finally, conifer nesters were most speciose in the north, decreasing in richness towards both the south, and the east (Figure IV-3).

Figure IV-1. The spatial distribution of the richness of ground nester species in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study.

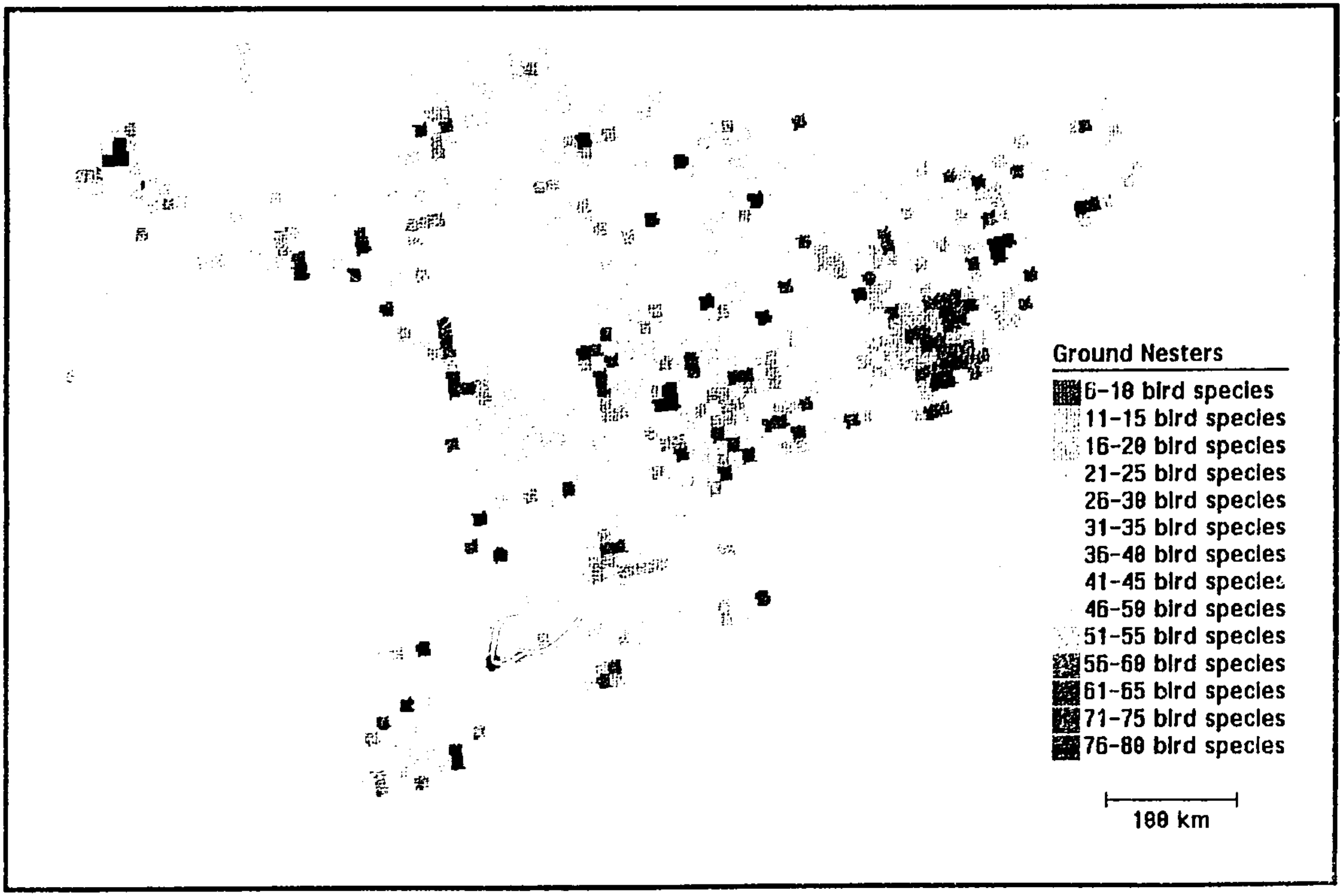

Ground Nesters
6-10 bird species
11-15 bird species
16-20 bird species
21-25 bird species
26-30 bird species
31-35 bird species
36-40 bird species
41-45 bird species
46-50 bird species
51-55 bird species
56-60 bird species
61-65 bird species
71-75 bird species
76-80 bird species
100 km

Figure IV-2. The spatial distribution of the richness of building nester bird species in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study.

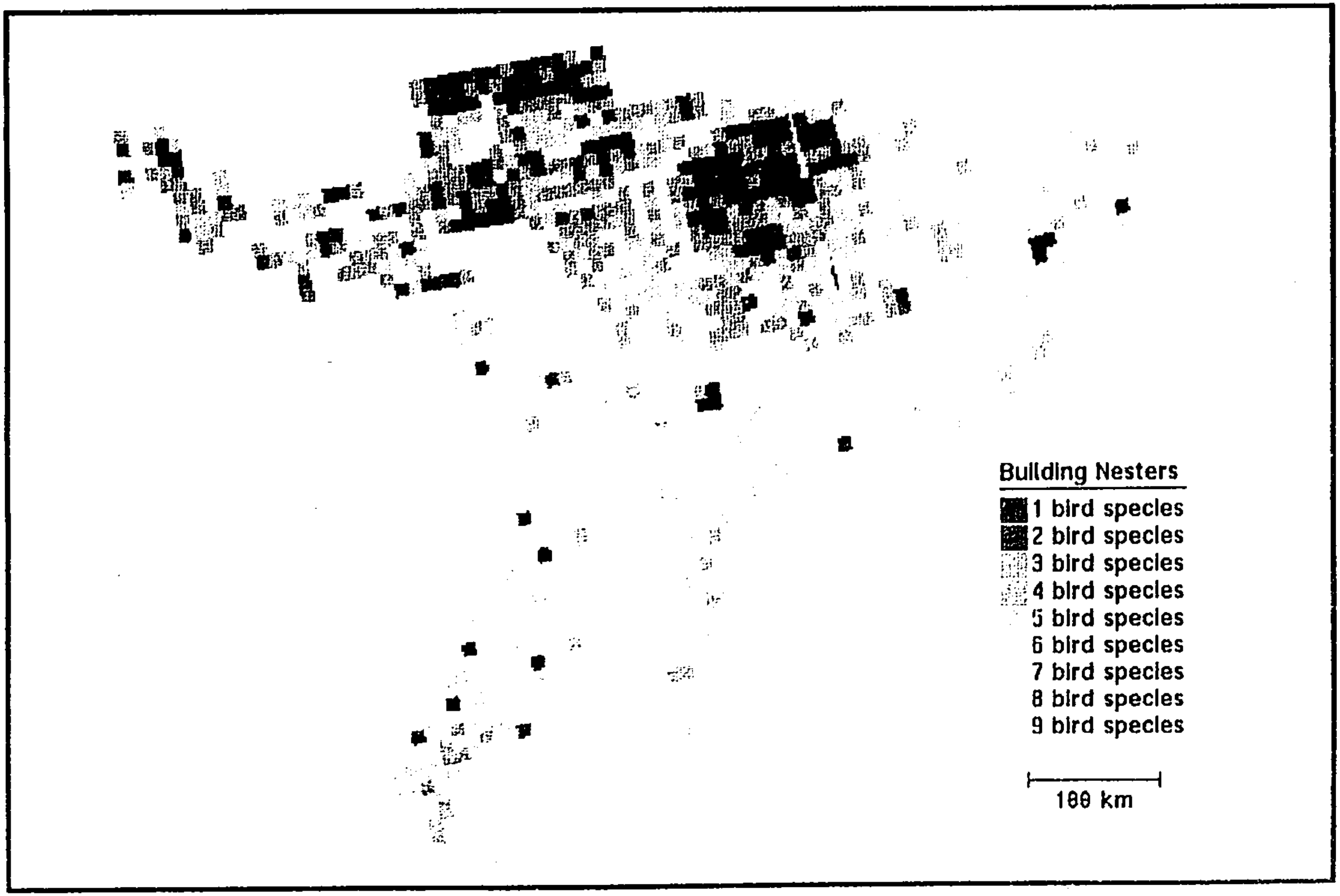
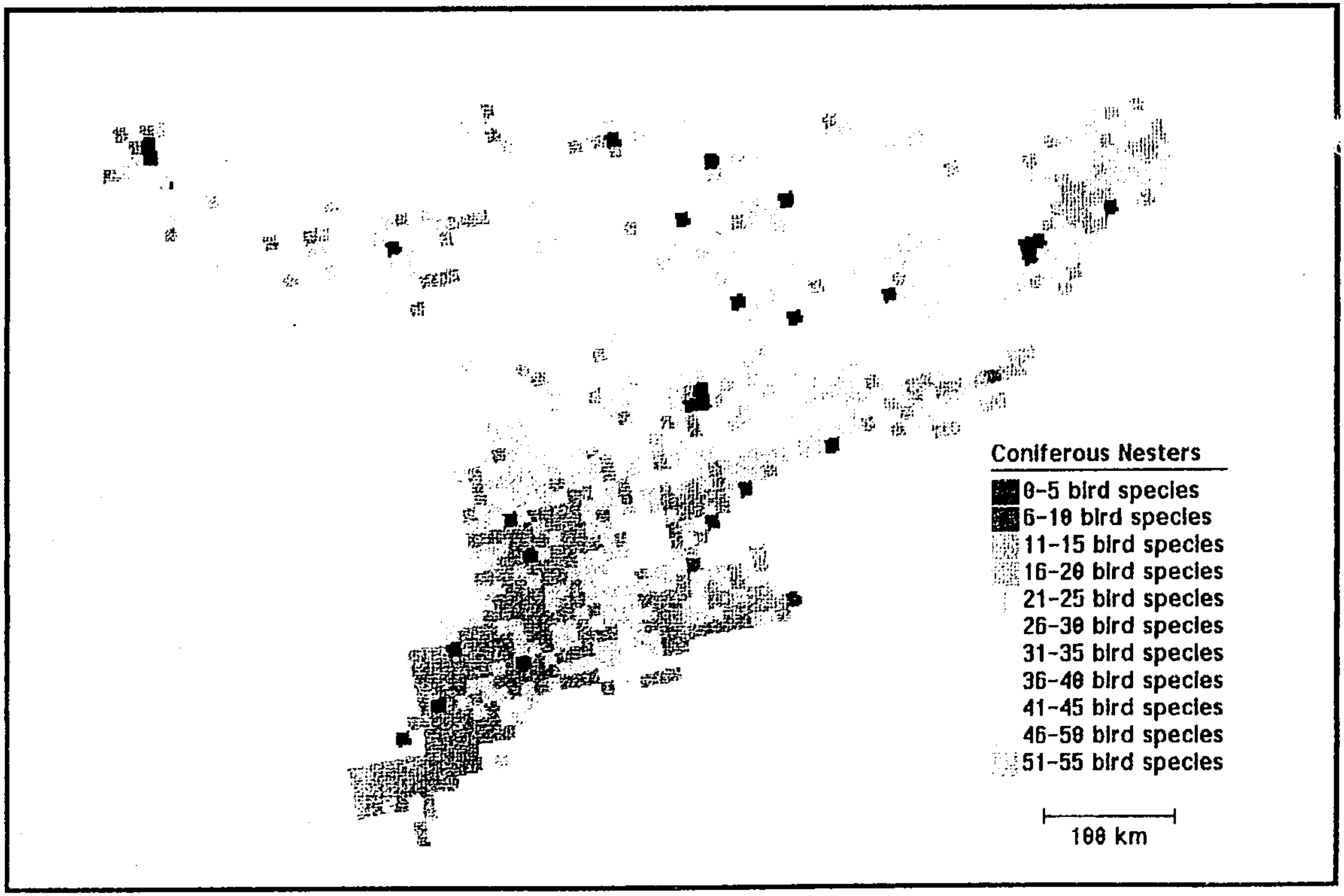

Building Nesters
1 bird species
2 bird species
3 bird species
4 bird species
5 bird species
6 bird species
7 bird species
8 bird species
9 bird species
100 km

Figure IV-3. The spatial distribution of the richness of conifer nester species in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study..


Coniferous Nesters
0-5 bird species
6-10 bird species
11-15 bird species
16-20 bird species
21-25 bird species
26-30 bird species
31-35 bird species
36-40 bird species
41-45 bird species
46-50 bird species
51-55 bird species
100 km

Guild richness - environment relationships were similar to, or stronger than, those previously computed between total richness and the environment (Chapter III). Depending on the particular guild examined, the strongest environmental correlate of richness explained between 12 and 54% of the variation in richness of any given guild (or 8 to 57% of the variation in guild richness, when the effects of observer hours were removed) (Tables IV-2 and IV-3). In comparison, the strongest individual environmental correlates of total avian species richness accounted for ≤13% of the variation in total avian species richness (Table III-1).

Similar results were observed when guild richness was related to multiple predictors. Variation in guild richness was similarly, or more adequately, explained in multiple polynomial regressions than that of total avian species richness. Between 33% and 65% of the variation in richness of different guilds was explained by multiple regressions whereas 38% of the variation in total avian species richness was accounted for (Appendix C).

The richness of the conifer nester guild had both the strongest relationships with the environmental predictors (Table IV-2 and Appendix C) and a very different spatial pattern than that of the other guilds (see above). A clear gradient in conifer richness appears as one crosses the limit of the pre-Cambrian Canadian Shield (Frontenac Axis) from either the south or the east (Figure IV-3). The number of coniferous nesting species increases across this ecotone where the poor acidic soils, granitic geology and boreal forest of the Canadian Shield replace the more fertile soils, maple-beech hardwood forests and agriculture of the St. Lawrence Lowlands.

Table IV-2. The amount of variation in avian guild richness (R^2_{adj}) explained by polynomial regressions (deg) (up to third degree) of selected environmental variables in 100 km^2 UTM squares over southern Ontario, Canada. All relationships significant at $p<0.001$, except those denoted by * where $0.05>p>0.001$. Non-significant relationships are denoted n.s.

	Snag nesters		Conifer nesters		Deciduous nesters		Shrub nesters		Ground nesters		Building nesters		Residents/ short dist. migrants		Long distance migrants	
	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg
Observer hours	0.21	2	0.01	3	0.27	2	0.24	2	0.24	2	0.15	2	0.27	2	0.11	3
Mean annual temperature (°C)	0.11	2	0.47	3	0.16	2	0.17	2	0.18	2	0.40	2	0.12	2	0.13	2
Total forest (km^2)	0.03	3	0.54	3	0.05	3	0.07	3	0.08	3	0.16	1	0.06	3	0.2	3
Surface water (km^2)	0.04	1	0.08	3	0.07	2	0.03	1	0.04	2	0.02	1	0.07	2	0.08	2
Agriculture (km^2)	0.05	2	0.41	3	0.08	2	0.14	2	0.14	2	0.32	3	0.10	2	0.09	3
Heterogeneity (H')	0.01	1	0.03	2	0.03	1	0.03	1	0.06	1	0.01	1	0.06	1	0.04	2
Human population	0.06	2	0.23	3	0.09	2	0.13	1	0.12	2	0.42	1	0.06	2	0.02	2
Park area (ha)	0.02	2	0.09	2	0.03	2	0.04	2	0.04	2	0.14	2	0.02	2	0.01	1
Soil fertility (exchang. bases)	0.11	3	0.28	3	0.09	3	0.11	3	0.11	3	0.29	3	0.06	3	0.03	1

Table IV-3. The amount of variation in avian guild richness (R^2_{adj}) explained by polynomial regressions (deg) (up to third degree) of selected environmental variables, controlling for the effect of observer hours, in 100 km² UTM squares over southern Ontario, Canada. All relationships significant at $p<0.001$, except those denoted by * where $0.05>p>0.001$. Non-significant relationships are denoted n.s.

	Snag nesters		Conifer nesters		Deciduous nesters		Shrub nesters		Ground nesters		Building nesters		Residents/ short dist. migrants		Long distance migrants	
	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg	R^2_{adj}	deg
Mean annual temperature (°C)	0.05	2	0.54	2	0.07	3	0.09	2	0.10	2	0.30	2	*0.01	1	0.20	3
Total forest (km²)	0.02	2	0.57	2	0.02	2	0.02	3	0.03	3	0.14	2	0.05	2	0.26	3
Suface water (km²)	0.05	3	0.05	2	0.04	1	0.04	3	0.02	2	0.02	1	0.04	2	0.04	1
Agriculture (km²)	*0.01	2	0.42	3	*0.00	2	0.05	2	0.04	2	0.21	2	0.02	3	0.12	2
Heterogeneity (H')	*0.00	1	0.02	2	0.01	1	0.01	1	0.04	1	n.s.	--	0.04	1	0.03	2
Human population	0.02	3	0.25	2	0.03	3	0.06	2	0.05	3	0.36	2	0.01	3	0.03	2
Park area (ha)	n.s.	--	*0.01	3	n.s.	--	n.s.	--	n.s.	--	n.s.	--	n.s.	--	n.s.	--
Soil fertility (exchang. bases)	0.05	3	0.3	3	0.03	2	0.05	3	0.04	3	0.22	3	0.01	2	0.05	2

The variation in conifer nesters was strongly positively related to the amount of total forest cover (Figure IV-4) (R^2_{adj}=0.54; R^2_{adj}=0.57 with observer hours controlled), and strongly negatively related to temperature variables (Table IV-2). Unlike the other measures of guild richness, the variation in conifer nesters was only very weakly related to observer hours and the amount of variation in conifer nester richness explained by the environmental variables increased after controlling for observer effort (Table IV-3).

In order to estimate the amount of variation in conifer richness individually attributable to forest area and temperature, we calculated the amount of conifer nester richness explained by both variables and subtracted the amount of variation explained by each predictor individually. Together forest and temperature explain 58.4% of the variation in conifer nesting richness (63.6% of the variation when observer hours are controlled) but due to their high degree of covariation (Table II-2), only 9% can be specifically attributed to forest area and 4.2% to temperature.

Not surprisingly, the squares with the most building nesting species lie along the more densely populated and urbanised southern edge of the study area (Figure IV-2). Predictably, there are fewer species of building nesters found in the far north of the study area where there are fewer buildings.

Even though only nine species made up the building nester guild, about 40% of the variation in building nester richness could be attributed to human population (Figure IV-5) (R^2_{adj}=0.42; R^2_{adj}=0.36 with observer hours controlled) or mean annual temperature (R^2_{adj}=0.40; R^2_{adj}=0.30 with observer hours controlled). Population and temperature covary (Table II-2), but both remain significant as terms in a multiple

Figure IV-4. The relationship between the richness of conifer nesters and the total amount of forest area in 100 km^2 UTM squares over southern Ontario, Canada. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).

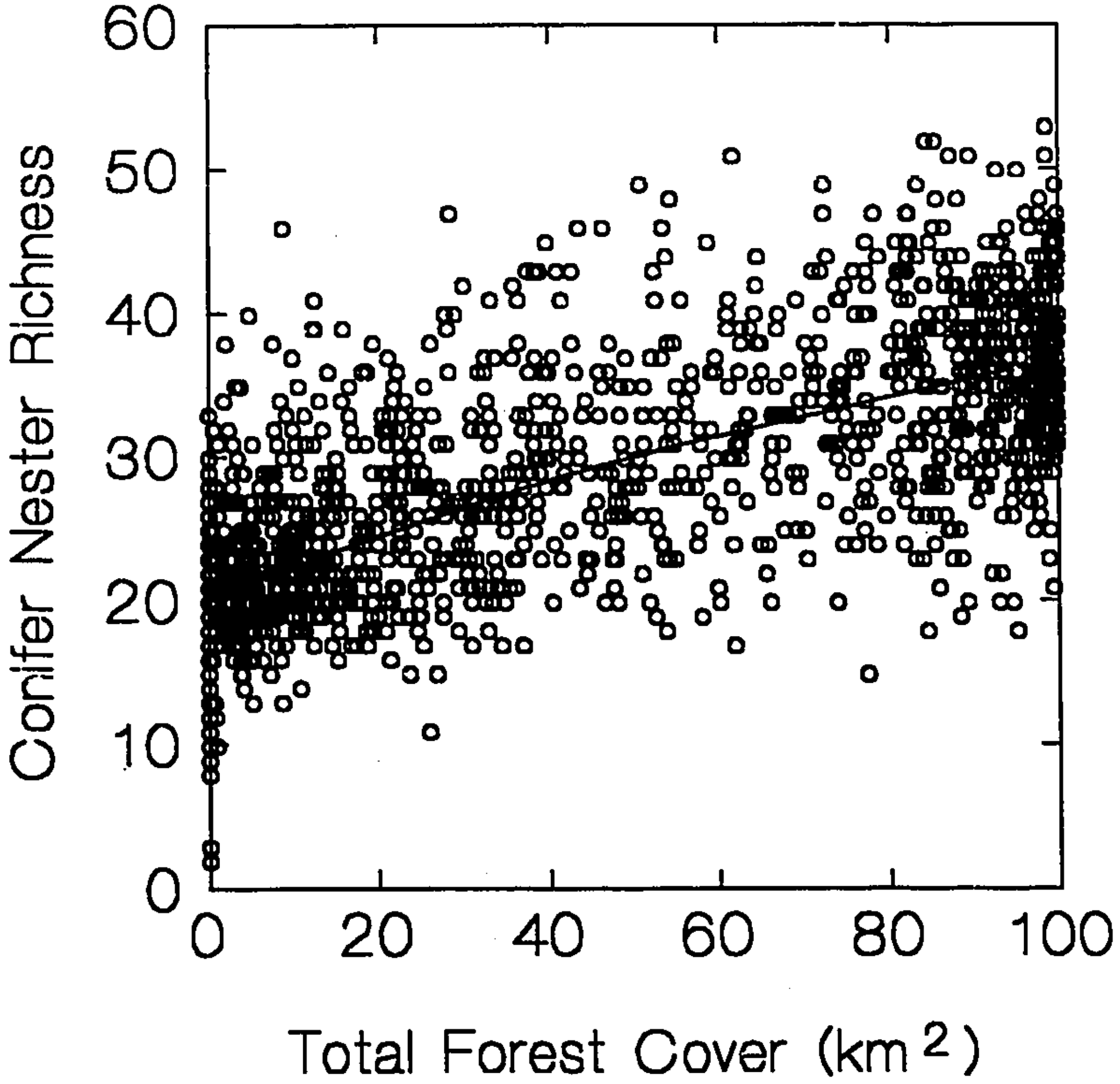
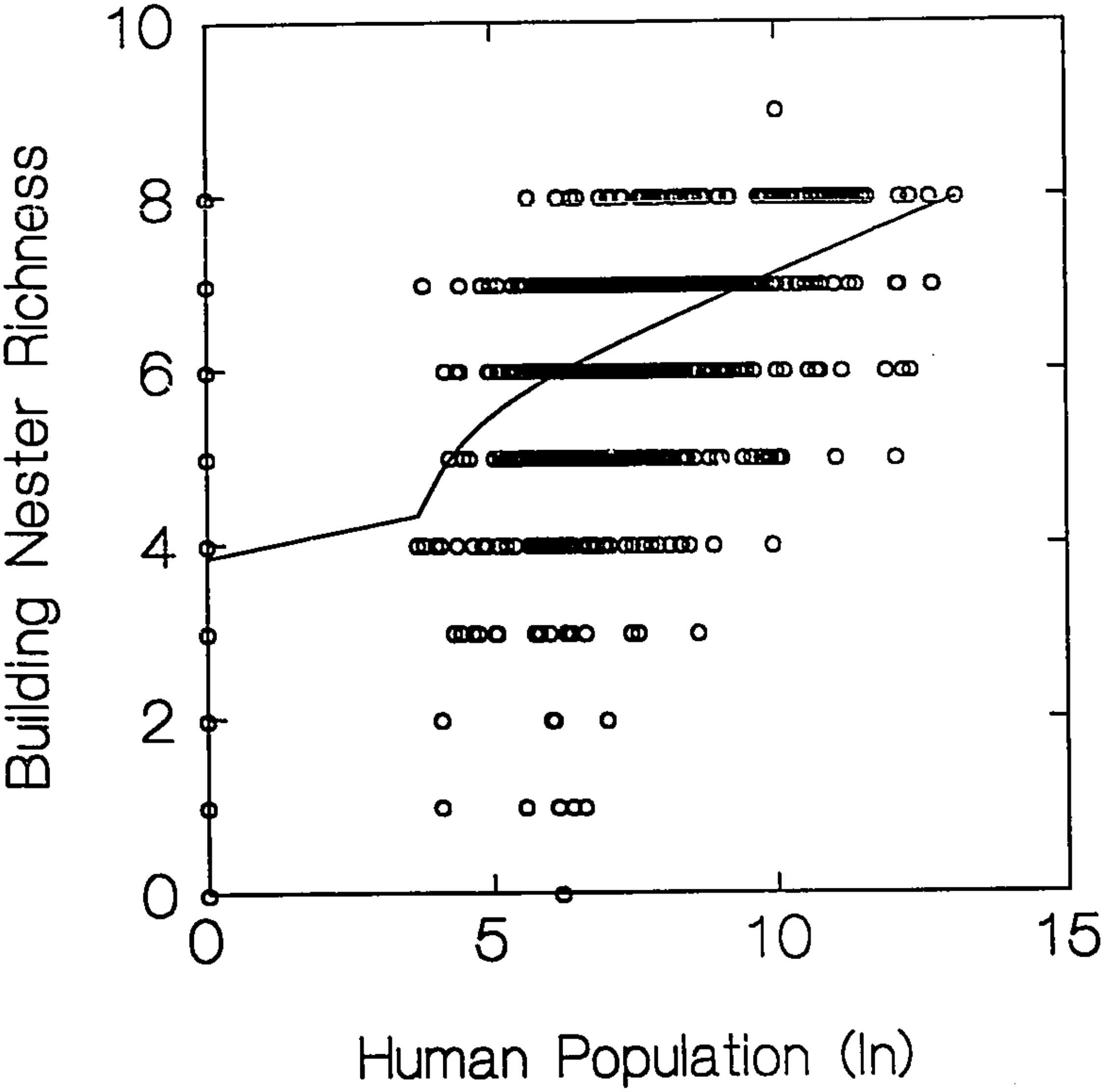

Conifer Nester Richness
60
50
40
30
20
10
0
0
20
40
60
80
100
Total Forest Cover (km²)

Figure IV-5. The relationship between the richness of building nesters and the human population in 100 km^2 UTM squares over southern Ontario, Canada. A LOWESS curve, calculating locally weighted regressions (tension =0.7), was plotted to represent the general trend in the data (Cleveland 1979).

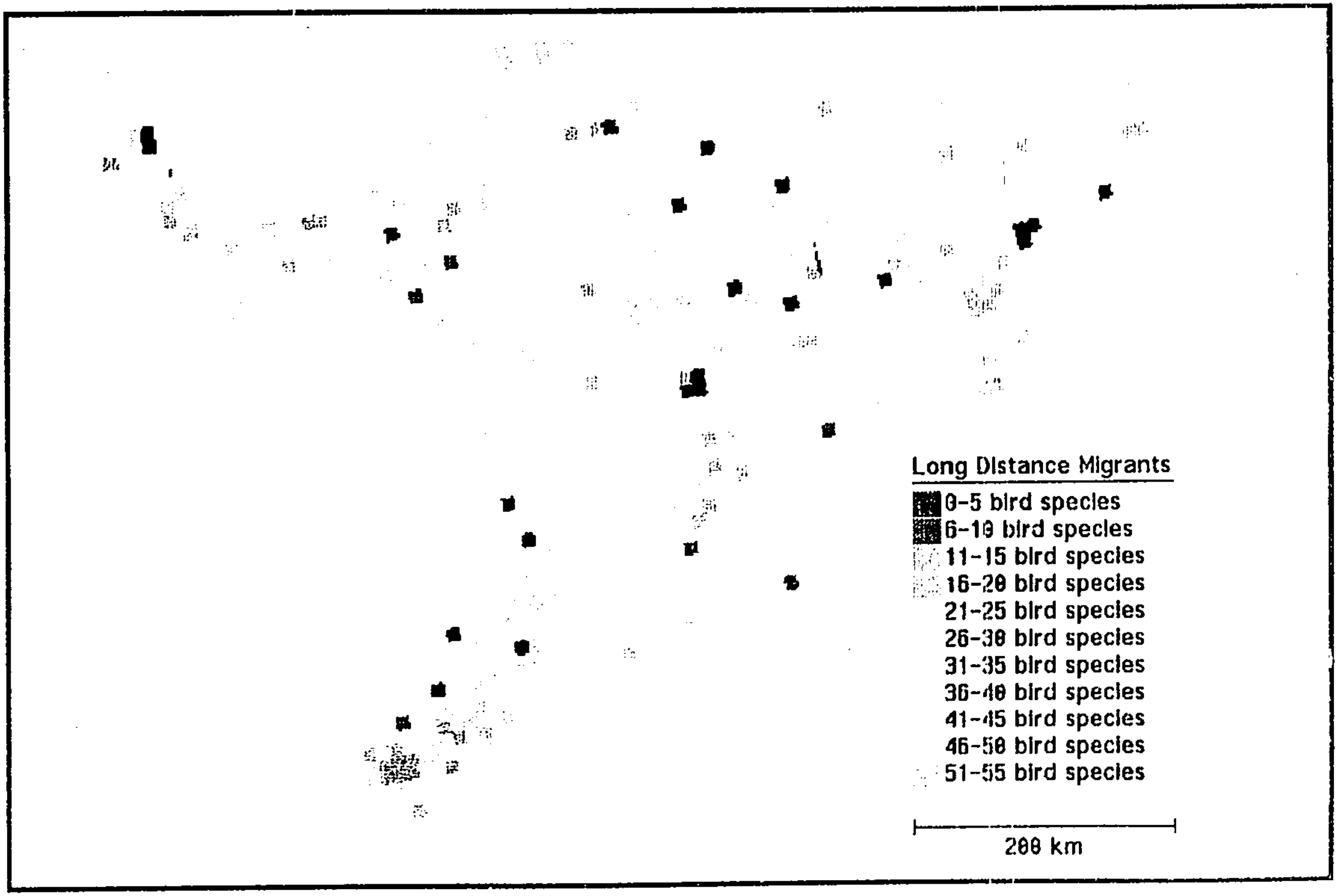

Building Nester Richness
Human Population (ln)
0
2
4
6
8
10
0
5
10
15

regression explaining 55.7% of the variation in building nester richness (Appendix C). The exact strength of these building richness - environment relationships is somewhat suspect because the richness data for building nesters do not exhibit stable variance, due in a large part, to the small number of species included in the guild.

Richness in the remaining four nesting guilds (deciduous nesters, ground nesters, shrub nesters, and snag nesters) and among residents/short distance migrants was distributed similarly to the distribution of total richness (Figure III-1, IV-1). In each case, the variation in richness was most strongly related to one of the temperature variables. For each guild, these relationships accounted for between 10 and 20% of the variation in richness (Tables IV-2 and IV-3). Controlling for observer hours weakened the relationships between the species richness of these guilds and the environmental characteristics because of the strong covariance between temperature and observer hours (Table II-2).

Long distance migrants were speciose both in the northern part of the study area and in the south-east (Figure IV-6). The species-rich area extending across northern portion of the study area resembled that exhibited by coniferous nesting species, and like conifer nester richness, long distance migrant richness was most strongly related to total forest area (R^2_{adj}=0.20, R^2_{adj}=0.26 when observed hours are controlled). After total forest area, the strongest individual correlates to long distance migrants were the number of forest classes and mean annual temperature, explaining 16 and 13% of the variation in richness respectively. Removing the effect of observer hours strengthened the richness - environment relationships.

Figure IV-6. The spatial distribution of the richness of long distance migrant species in 100 km^2 UTM squares over southern Ontario, Canada. Blackened squares lacked species information or sampling effort and were not included in this study.


Long Distance Migrants
0-5 bird species
6-10 bird species
11-15 bird species
16-20 bird species
21-25 bird species
26-30 bird species
31-35 bird species
36-40 bird species
41-45 bird species
46-50 bird species
51-55 bird species
200 km

Discussion

Previous research revealed that mean annual temperature and the total amount of forest cover were the best correlates of the total avian species richness in 100 km^2 squares over 200 000 km^2 of southern Ontario (Chapter III). However, these two predictors each explained only 8-13% of the variation in avian richness, and the relationships were not strong enough to suggest that total avian species richness might be caused by one or two environmental characteristics. Neither climatic variables, forest cover, nor surrogates for human impact (population) or a lack thereof (parkland), explained large amounts of the variation in total avian richness at this scale.

One possible explanation for the weakness of these relationships is that groups of species with differing life-history strategies may respond to environmental characteristics in very different ways, thus confounding the richness - environment relationships (e.g. Noon *et al.* 1980, Cody 1985). We therefore examined whether subsets of total avian richness, the species richness of life-history guilds, would be more closely related to environmental variables at regional spatial scales.

The spatial patterns of guild richness over southern Ontario did indeed vary according to the life-history guild examined. The strength of the relationships between guild richness and the environmental characteristics also varied depending on the life-history guild, but they were similar to, or stronger than those calculated for total avian richness. Temperature was one of the two strongest correlates guild richness for all guilds, but for most guilds explained only 10%-20% of the variation in richness. Certain guilds were found to be much more strongly related to specific environmental characteristics related to habitat.

We propose that these guild richness - environment relationships reflect a common pattern. The approximately constant relationship (10% to 20% of the variation) between the measures of richness and temperature suggests that temperature (energy) may influence the regional avian species pool. Strong richness - habitat relationships appear in those life-history guilds that require particular habitat characteristics, the availability of which is spatially variable. Otherwise, richness is most closely related to temperature, even though it might be reflection of processes acting at a larger spatial scale.

The richness of conifer nesters and building nesters was more strongly related to specific habitat characteristics, reflecting their life-histories, than to temperature. Conifer nester richness was most strongly related to total forest area, rather than to any particular forest type. Either the conifer nesters, as a guild, are not terribly particular about the type of forest they nest in, or all the different types of forest this study area could provide enough coniferous vegetation to support conifer nesting species. The major component of total forest cover was mixedwood forest (defined as pixels with >50% forest canopy, 26 to 75% of which was needle leaved) which makes up 86% of the forest over southern Ontario, and presumably represents appropriate habitat for conifer nesting species.

Building nester richness was most strongly related to human population, and to a lesser extent temperature. Finding more building nesting species in those areas that have more buildings, was not surprising, however it did increase our confidence in the methods and information used in the guild classification.

The richness of the other guilds were most strongly related to temperature, but the magnitudes of these relationships were only marginally stronger, if at all, than those calculated for total species richness. Why is the regional scale variation in richness for every life-history guild not strongly related to one, or more, specific habitat characteristics? One possibility is that the richness of some guilds was not very variable over the study area. Among the nesting guilds, the richness of conifer and building nesters was almost twice as variable as that of the other nesting guilds (mean C.V.=0.312, mean C.V. =0.185, N=1721), with the former exhibiting the strong richness - habitat relationships.

The weak habitat - guild richness relationships might also be due to relatively uniformly distributed habitat types over the study area. At least insofar as the AVHRR-LAC images can resolve habitat types, this is unlikely. The amount of area in land cover classes, per UTM square, was much more variable over the study area (C.V.'s from 0.33 to 28.7) than guild species richness.

It is also possible that AVHRR-LAC images, at a pixel resolution of 1 km^2, did not identify biologically relevant habitat types. Habitats such as shrubs, forest-interior, edge, shorelines and wetlands all occur over southern Ontario, but did not appear on the land cover image.

Another possible reason for weak guild richness - habitat relationships is that some guilds might not be defined in a biologically meaningful way. Our analyses suggest that if one would like to explain regional scale patterns of guild richness using environmental variables, then nesting habitat seems to be a better life-history trait on which to base guild classification than general migratory strategy. It is not clear however, to what extent modifying guild definitions would strengthen the guild richness - habitat relationships. It could be argued that conifer nesters and building nesters have relatively specific habitat requirements and this could have led to their strong richness - habitat relationships. This may be true, but simply using narrow "niches" as the basis for guild creation does not ensure strong richness - habitat relationships, since snag nesters, for example, have very particular nesting requirements and are only weakly related to any of the habitat variables we examined.

The potential problems arising from guild classification notwithstanding, some of the guilds studied were strongly related to habitat characteristics which, in turn, can be influenced by human activities. It is these life-history guilds, whose patterns of richness are not simply a reflection of larger scale richness - energy relationships that are of interest to conservation planners and environmental managers. It is critical to investigate which life-history characteristics define guilds strongly related to the availability of specific habitats, and furthermore establish whether causal relationships exist between these habitats and the richness of particular avian life-history guilds.

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CONCLUSIONS AND SPECULATIONS

This study represents the most comprehensive investigation of regional scale relationships between avian species richness and the environment to date. Access to the ABBO database, other digital data sources and a GIS, combined to make this study possible.

Total richness and the richness of all the life-history guilds varied spatially over southern Ontario. Both the magnitude of this variation and the strength of the richness - environment relationships were dependant on the group of species examined. Similar amounts of the variation in total richness and the richness of individual guilds could be attributed to temperature. We suggest that these relationships are a reflection of the larger-scale influence temperature has on the regional avian species pool. The relationships are weaker than those observed at larger scales for two reasons. Firstly, on sufficiently large scales (sufficiently large quadrats), species richness equates the regional species pool. Secondly, there is a wider range of temperatures over wider spatial extents.

Richness was also significantly related to habitat characteristics, but these relationships were relatively weak, except in the case of conifer nester richness and building nester richness. Up to four times as much of the variation in the richness of these two guilds, relative to total richness, can be attributed to individual characteristics of the environment. We propose that these strong richness - habitat relationships only appear in those life-history guilds that require particular habitat characteristics, the availability of which is spatially variable. Otherwise, the temperature effects on the species pool appear to predominate, as was the case for the other life-history guilds and for total avian species richness.

It seems reasonable to propose that more building nester species occur where there are more buildings, and even, that more coniferous nesting species will be found in areas with more forest. But why is total richness and the other life-history guilds, especially groups like deciduous nesters, not strongly related to a particular habitat types?

We suspect that strength of observed richness-environment relationships strongly depends upon spatial scale. Total richness is not strongly related to habitat availability at large spatial scales because, at sufficiently large spatial scales, nearly all the quadrats contain nearly all of the habitat types. Consequently, the relationships between total richness and habitat disappear. What then becomes important is the energy input and the ability of an area to capture that energy. Climatic energy is sufficiently well related to the energy requirements of particular species to provide a 'common currency' for all species, and large scale patterns of richness are related to variables like PET and temperature.

At intermediate spatial scales, richness-climate relationships are much weaker because the processes that are thought to cause observed patterns of total species richness operate at spatial scales larger than the scale of this study. Furthermore, climate is much less variable over the less extensive study areas. In contrast, habitat availability can begin to vary among quadrats. There is no longer a 'common currency' among dissimilar species, since different species can use profoundly dissimilar habitats. By grouping species into guilds with similar habitat requirements, one can test whether increased habitat availability is related to increased richness (as opposed to increased abundance in a constant number of species). Our results suggest that guild richness does indeed increase with increased habitat availability.

So why is the richness of most of the life-history guilds not strongly related to a particular aspects of habitat? We do not have a definitive answer to that question. The richness of nesting guilds weakly related to habitat, tended to be less variable over the study area, potentially weakening guild richness - habitat relationships. Alternatively, the AVHRR-LAC image might not be capable of measuring available habitat due to an inappropriate pixel resolution or because land cover might simply not correspond to available habitat for some guilds. Only conifer nester richness is strongly related to the remotely-sensed land cover information. Building nester richness is only weakly related to urban area, as portrayed on the AVHRR-LAC image, whereas the more detailed census information reveals a strong richness-human population relationship. The resolution and character of the AVHRR-LAC imagery is only sufficient to measure available habitat in particular guilds.

Migratory guilds were more variable over the study area, but not substantially more strongly related to habitat characteristics. There may be less of an *a priori* reason to expect strong migratory guild richness - habitat correlations, compared to the nesting guild richness - habitat relationships. Nonetheless we do not have an adequate explanation why the richness of these migratory guilds shows strong spatial patterns, and yet it is not strongly related to the availability of particular habitats.

From a conservation planning and management perspective, guild richness appears to be a much more useful measure of biological diversity, on regional spatial scales, than total avian species richness. Nesting habitat preference seems to be a more appropriate life-history trait than general migratory strategy to base a guild classification system on. Further research should continue to identify life-history guilds that are closely related to the availability of particular habitat types. Manipulation of the habitats can then be to test hypotheses about causal relationships between habitat availability and avian guild richness.

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APPENDIX A. Classification of the bird species found in southern Ontario into life history guilds. Species were associated with one or more types of habitat in which their nests were commonly found: tree snags (**snag**), coniferous forest (**conif**), deciduous forest (**decid**), shrubs (including grass) (**shrub**), ground (including floating, cliffs and banks) (**ground**) and buildings (**building**). Species were differentiated as either long-distance migrants (wintering south of the Gulf of Mexico) (**long-d**) or as residents/short-distance migrants (**resident**). Species were also assigned to non-exclusive, food guilds based on the types of food preferentially consumed: vertebrates (**verts**), terrestrial invertebrates (**t-invert**), aquatic invertebrates (**a-invert**), fruit (including grains, nectar and sap) (**fruit**), nut (including seeds) (**nut**) and omnivorous (**omni**). A '1' indicates inclusion in the life-history guild.

Common Name	Species Code	Nesting Habitat						Migratory Strategy		Food Preference					
		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Acadian flycatcher	ACFL	0	1	1	1	0	0	0	1	0	1	0	0	0	0
Alder flycatcher	ALFL	0	0	0	1	0	0	0	1	0	1	0	0	0	0
American bittern	AMBI	0	0	0	0	1	0	1	0	1	0	0	0	0	0
American coot	AMCO	0	0	0	0	1	0	1	0	0	0	0	0	0	1
American goldfinch	AMGO	0	0	0	1	0	0	1	0	0	0	0	0	1	0
American kestrel	AMKE	1	1	1	0	1	0	1	0	0	1	0	0	0	0
American redstart	AMRE	0	0	1	1	0	0	0	1	0	1	0	0	0	0
American robin	AMRO	0	1	1	0	0	0	1	0	0	1	0	0	0	0
American wigeon	AMWI	0	0	0	0	1	0	1	0	0	0	0	1	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
American woodcock	AMWO	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Bald eagle	BAEA	0	1	0	0	1	0	1	0	1	0	0	0	0	0
Barn owl	BAOW	1	1	1	0	0	1	1	0	1	0	0	0	0	0
Barn swallow	BASW	0	0	0	0	0	1	1	0	0	1	0	0	0	0
Black-billed cuckoo	BBCU	0	0	1	1	0	0	1	0	0	1	0	0	0	0
Black-backed three-toed woodpecker	BBTW	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Bay-breasted warbler	BBWA	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Black-capped chickadee	BCCH	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Black-crowned night-heron	BCNH	0	0	1	1	0	0	1	0	1	0	0	0	0	0
Barred owl	BDOW	1	1	1	0	0	0	1	0	1	0	0	0	0	0
Belted kingfisher	BEKI	1	0	0	0	1	0	0	1	1	0	0	0	0	0
Blue-grey gnatcatcher	BGGN	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Brown-headed cowbird	BHCO	0	0	1	1	1	0	0	1	0	1	0	0	0	0
Bank swallow	BKSW	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Black duck	BLDU	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Blue jay	BLJA	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Black tern	BLTE	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Blue-winged warbler	BLUE	0	0	0	1	1	0	0	1	0	1	0	0	0	0
Blackburnian warbler	BLWA	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Bobolink	BOBO	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Bobwhite	BOBW	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Boreal chickadee	BOCH	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Brewer's blackbird	BRBL	0	1	0	1	1	0	0	1	0	1	0	0	0	0
Brown creeper	BRCR	0	1	1	0	0	0	1	0	0	1	0	0	0	0
Brown thrasher	BRTH	0	0	0	1	1	0	1	0	0	0	0	0	0	1

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Brewster's warbler	BRWA	0	0	0	1	1	0	0	1	0	1	0	0	0	0
Black-throated blue warbler	BTBW	0	1	0	1	0	0	1	0	0	1	0	0	0	0
Black-throated green warbler	BTGW	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Bufflehead	BUFF	1	1	1	0	1	0	1	0	0	0	1	0	0	0
Broad-winged hawk	BWHA	0	0	1	0	0	0	0	1	1	0	0	0	0	0
Blue-winged teal	BWTE	0	0	0	0	1	0	0	1	0	0	0	0	1	0
Black-and-white warbler	BWWA	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Canada goose	CAGO	0	0	0	0	1	0	1	0	0	0	0	1	0	0
California gull	CAGU	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Canvasback	CANV	0	0	0	0	1	0	1	0	0	0	1	1	0	0
Cardinal	CARD	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Caspian tern	CATE	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Canada warbler	CAWA	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Carolina wren	CAWR	1	0	1	0	0	0	1	0	0	1	0	0	0	0
Clay-coloured sparrow	CCSP	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Cerulean warbler	CEWA	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Cedar waxwing	CEWX	0	1	1	0	0	0	1	0	0	0	0	1	0	0
Chipping sparrow	CHSP	0	1	1	0	0	0	0	1	0	1	0	0	0	0
Chimney swift	CHSW	0	0	0	0	0	1	0	1	0	1	0	0	0	0
Cinnamon teal	CITE	0	0	0	0	1	0	0	1	0	0	0	0	1	0
Cliff swallow	CLSW	0	0	0	0	1	1	0	1	0	1	0	0	0	0
Cape may warbler	CMWA	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Common crow	COCR	0	0	1	1	0	0	1	0	0	0	0	0	0	1
Common flicker	COFL	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Common gallinule	COGA	0	0	0	0	1	0	0	1	0	0	0	0	0	1

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Common goldeneye	COGO	1	1	1	0	1	0	1	0	0	0	1	0	0	0
Common grackle	COGR	0	1	1	0	0	0	1	0	0	0	0	0	0	1
Cooper's hawk	COHA	0	1	1	0	0	0	0	1	1	0	0	0	0	0
Common loon	COLO	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Common merganser	COME	0	0	1	0	1	0	1	0	1	0	0	0	0	0
Common nighthawk	CONI	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Common raven	CORA	0	1	0	0	1	0	1	0	0	0	0	0	0	1
Common snipe	COSN	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Common tern	COTE	0	0	0	0	1	0	0	1	1	0	0	0	0	0
Connecticut warbler	COWA	0	0	0	1	1	0	0	1	0	1	0	0	0	0
Common yellowthroat	COYE	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Chestnut-sided warbler	CSWA	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Chuck-will's-widow	CWWI	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Double-crested cormorant	DCCO	0	1	1	0	1	0	1	0	1	0	0	0	0	0
Dark-eyed junco	DEJU	0	0	0	0	1	0	0	1	0	0	0	0	1	0
Dickcissel	DICK	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Downy woodpecker	DOWO	1	0	1	0	0	0	1	0	0	1	0	0	0	0
Eastern bluebird	EABL	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Eastern kingbird	EAKI	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Eastern meadowlark	EAME	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Eastern phoebe	EAPH	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Evening grosbeak	EVGR	0	1	1	0	0	0	1	0	0	0	0	0	1	0
Eastern wood pewee	EWPE	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Field sparrow	FISP	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Forster's tern	FOTE	0	0	0	0	1	0	1	0	1	0	0	0	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Gadwall	GADW	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Great black-backed gull	GBBG	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Great blue heron	GBHE	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Great-crested flycatcher	GCFL	1	0	1	0	0	0	0	1	0	1	0	0	0	0
Golden-crowned kinglet	GCKI	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Great horned owl	GHOW	0	1	1	0	1	0	1	0	1	0	0	0	0	0
Goshawk	GOSH	0	1	1	0	0	0	1	0	1	0	0	0	0	0
Gray catbird	GRCA	0	0	0	1	0	0	0	1	0	1	0	0	0	0
Great egret	GREG	0	0	1	1	0	0	1	0	1	0	0	0	0	0
Green heron	GRHE	0	0	1	1	0	0	0	1	1	0	0	0	0	0
Gray jay	GRJA	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Gray partridge	GRPA	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Grasshopper sparrow	GRSP	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Green-winged teal	GWTE	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Golden-winged warbler	GWWA	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Hairy woodpecker	HAWO	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Herring gull	HEGU	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Henslow's spparrow	HESP	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Hermit thrush	HETH	0	1	1	0	1	0	1	0	0	1	0	0	0	0
House finch	HOFI	0	0	1	1	0	1	1	0	0	0	0	0	1	0
Horned lark	HOLA	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Hooded merganser	HOME	1	1	1	0	0	0	1	0	1	0	0	0	0	0
House sparrow	HOSP	0	1	1	0	0	1	1	0	0	0	0	0	1	0
Hooded warbler	HOWA	0	0	0	1	0	0	0	1	0	1	0	0	0	0
House wren	HOWR	1	0	1	0	0	0	1	0	0	1	0	0	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Indigo bunting	INBU	0	0	1	1	0	0	1	0	0	1	0	0	0	0
Kentucky warbler	KEWA	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Killdeer	KILL	0	0	0	0	1	0	1	0	0	1	0	0	0	0
King rail	KIRA	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Kirtland's warbler	KIWA	0	1	0	0	1	0	0	1	0	1	0	0	0	0
Lawrence's warbler	LAWA	0	0	0	1	1	0	0	1	0	1	0	0	0	0
LeConte's sparrow	LCSP	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Least bittern	LEBI	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Least flycatcher	LEFL	0	1	0	1	0	0	1	0	0	1	0	0	0	0
Long-eared owl	LEOW	0	1	1	0	1	0	1	0	1	0	0	0	0	0
Lesser scaup	LESC	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Lesser yellowlegs	LIGU	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Lincoln's sparrow	LISP	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Loggerhead shrike	LOSH	0	1	0	1	0	0	0	1	0	1	0	0	0	0
Louisiana waterthrush	LOWA	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Marsh hawk	MAHA	0	0	0	1	1	0	1	0	1	0	0	0	0	0
Mallard	MALL	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Magnolia warbler	MAWA	0	1	0	1	0	0	0	1	0	1	0	0	0	0
Marsh wren	MAWR	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Merlin	MERL	0	0	1	0	1	0	0	1	1	0	0	0	0	0
Mockingbird	MOCK	0	1	1	1	0	0	1	0	0	1	0	0	0	0
Mourning dove	MODO	0	1	1	0	1	0	1	0	0	0	0	0	1	0
Mourning warbler	MOWA	0	0	0	1	1	0	0	1	0	1	0	0	0	0
Mute swan	MUSW	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Nashville warbler	NAWA	0	0	0	0	1	0	0	1	0	1	0	0	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Northern oriole	NOOR	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Northern shoveler	NOSH	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Northern three-toed woodpecker	NOTW	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Northern waterthrush	NOWA	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Northern parula warbler	NPWA	0	1	1	0	0	0	0	1	0	1	0	0	0	0
Orchard oriole	OROR	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Olive-sided flycatcher	OSFL	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Osprey	OSPR	0	1	1	0	1	0	0	1	1	0	0	0	0	0
Ovenbird	OVEN	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Palm warbler	PAWA	0	1	0	0	1	0	0	1	0	1	0	0	0	0
Pied-billed grebe	PBGR	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Peregrine falcon	PEFA	0	1	1	0	1	0	0	1	1	0	0	0	0	0
Philadelphia vireo	PHVI	0	1	1	1	0	0	0	1	0	1	0	0	0	0
Pine grosbeak	PIGR	0	1	0	1	0	0	1	0	0	0	0	0	1	0
Pintail	PINT	0	0	0	0	1	0	1	0	0	0	0	0	1	0
Piping plover	PIPL	0	0	0	0	1	0	1	0	0	0	1	0	0	0
Pine siskin	PISI	0	1	1	0	0	0	1	0	0	0	0	0	1	0
Pine warbler	PIWA	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Pileated woodpecker	PIWO	1	1	0	0	0	0	1	0	0	1	0	0	0	0
Prairie warbler	PRWA	0	1	0	1	0	0	0	1	0	1	0	0	0	0
Prothonotary warbler	PTWA	1	1	1	0	0	0	0	1	0	1	0	0	0	0
Purple finch	PUFI	0	1	1	0	0	0	1	0	0	0	0	0	1	0
Purple gallinule	PUGA	0	0	0	0	1	0	0	1	0	0	0	0	0	1
Purple martin	PUMA	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Rose-breasted grosbeak	RBGR	0	0	1	1	0	0	0	1	0	1	0	0	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Ring-billed gull	RBGU	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Red-breasted merganser	RBME	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Red-breasted nuthatch	RBNU	0	1	0	0	0	0	1	0	0	1	0	0	0	0
Red-bellied woodpecker	RBWO	1	0	1	0	0	0	1	0	0	1	0	0	0	0
Ruby-crowned kinglet	RCKI	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Red crossbill	RECR	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Redhead	REDH	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Red-eyed vireo	REVI	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Red-headed woodpecker	RHWO	1	0	1	0	0	0	1	0	0	0	0	0	0	1
Ring-necked duck	RNDU	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Red-necked grebe	RNGR	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Ring-necked pheasant	RNPH	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Rock dove	RODO	0	0	0	0	1	1	1	0	0	0	0	0	1	0
Red-shouldered hawk	RSHA	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Rufous-sided towhee	RSTO	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Red-tailed hawk	RTHA	0	0	1	0	1	0	1	0	1	0	0	0	0	0
Ruby-throated hummingbird	RTHU	0	0	1	0	0	0	0	1	0	0	0	1	0	0
Rusty blackbird	RUBL	0	1	0	1	0	0	1	0	0	1	0	0	0	0
Ruddy duck	RUDU	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Ruffed grouse	RUGR	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Red-winged blackbird	RWBL	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Rough-winged swallow	RWSW	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Sandhill crane	SACR	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Savannah sparrow	SASP	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Screech owl	SCOW	1	0	1	0	0	0	1	0	0	1	0	0	0	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Scarlet tanager	SCTA	0	0	1	0	0	0	0	1	0	1	0	0	0	0
Short-eared owl	SEOW	0	0	0	0	1	0	1	0	1	0	0	0	0	0
Sedge wren	SEWR	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Sora	SORA	0	0	0	0	1	0	1	0	0	0	0	1	1	0
Solitary sandpiper	SOSA	0	1	1	0	0	0	1	0	0	1	0	0	0	0
Song sparrow	SOSP	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Solitary vireo	SOVI	0	1	1	0	0	0	1	0	0	1	0	0	0	0
Spruce grouse	SPGR	0	0	0	0	1	0	0	1	0	0	0	1	0	0
Spotted sandpiper	SPSA	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Sharp-shinned hawk	SSHA	0	1	1	0	0	0	0	1	1	0	0	0	0	0
Starling	STAR	0	0	1	0	0	1	1	0	0	1	0	0	0	0
Sharp-tailed grouse	STGR	0	0	0	0	1	0	1	0	0	0	0	1	0	0
Summer tanager	SUTA	0	1	1	0	0	0	1	0	0	1	0	0	0	0
Saw-whet owl	SWOW	1	1	0	0	0	0	1	0	1	0	0	0	0	0
Swamp sparrow	SWSP	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Swainson's thrush	SWTH	0	1	0	1	0	0	1	0	0	1	0	0	0	0
Tennessee warbler	TEWA	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Tree swallow	TRSW	1	1	1	0	0	0	1	0	0	1	0	0	0	0
Turkey	TURK	0	0	0	0	1	0	1	0	0	0	0	0	0	1
Tufted titmouse	TUTI	1	0	1	0	0	0	0	1	0	1	0	0	0	0
Turkey vulture	TUVU	1	1	1	0	1	0	1	0	1	0	0	0	0	0
Upland sandpiper	UPSA	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Veery	VEER	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Vesper sparrow	VESP	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Virginia rail	VIRA	0	0	0	0	1	0	1	0	0	1	0	0	1	0

		snag	conif	decid	shrub	ground	building	resident	long-d	verts	t-invert	a-invert	fruit	nut	omni
Warbling vireo	WAVI	0	0	1	1	0	0	1	0	0	1	0	0	0	0
White-breasted nuthatch	WBNU	0	0	1	0	0	0	1	0	0	1	0	0	0	0
Western meadowlark	WEME	0	0	0	0	1	0	1	0	0	1	0	0	0	0
White-eyed vireo	WEVI	0	0	0	1	0	0	1	0	0	1	0	0	0	0
Willow flycatcher	WIFL	0	0	1	1	0	0	0	1	0	1	0	0	0	0
Wilson's phalarope	WIPH	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Wilson's warbler	WIWA	0	0	0	1	1	0	1	0	0	1	0	0	0	0
Winter wren	WIWR	1	1	0	0	0	0	0	1	0	1	0	0	0	0
Wood duck	WODU	1	1	1	0	0	0	0	1	0	0	1	0	0	0
Wood thrush	WOTH	0	1	1	0	0	0	1	0	0	1	0	0	0	0
Whip-poor-will	WPWI	0	0	0	0	1	0	0	1	0	1	0	0	0	0
White-throated sparrow	WTSP	0	0	0	1	0	0	1	0	0	0	0	0	0	0
White-winged crossbill	WWCR	0	0	0	0	1	0	0	1	0	1	0	0	0	0
Yellow-breasted chat	YBCH	0	0	0	1	0	0	1	0	0	0	1	0	0	0
Yellow-billed cuckoo	YBCU	0	0	1	1	0	0	1	0	0	1	0	0	0	0
Yellow-bellied flycatcher	YBFL	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Yellow-bellied sapsucker	YBSA	0	1	1	0	0	0	0	1	0	1	0	0	0	0
Yellow rail	YERA	0	0	0	0	1	0	0	1	0	0	1	0	0	0
Yellow warbler	YEWA	0	1	1	1	0	0	1	0	0	1	0	0	0	0
Yellow-headed blackbird	YHBL	0	0	0	0	1	0	1	0	0	1	0	0	0	0
Yellow-rumped warbler	YRWA	0	1	0	0	0	0	0	1	0	1	0	0	0	0
Yellow-throated warbler	YTVI	0	0	1	0	0	0	0	1	0	1	0	0	0	0

APPENDIX B. Comparison of ordinary least squares multiple linear regression models and generalised linear models, using a Poisson-distributed error term and a log link function, relating the species richness variables to characteristics of the environment. For both analyses, predictors variables were incorporated into the models using stepwise addition, and they are presented below in order of decreasing T-value. Abreviations used for the predictor variables in the text are defined below (also see Methods, Table II-1).

AGRICULT= Agricultural land area
BUILTUP= Built-up area
HETEROGE= Heterogeneity
NOFOREST= Number of forest classes
OBSHOURS= ln(Observer hours)
PDYSNOW= Days of snowfall
POP= ln(Human population)
PRKAREA= ln(Park area)
PSNWCOV5= Number of days with 5cm of snow cover
PTOTSNOW= Total snowfall
SOILFERT= Soil fertility
TMPMEAN= Mean annual temperature
TOTFORES= Total forest cover
WATER= Surface water area

TOTAL AVIAN SPECIES RICHNESS

ORDINARY LEAST SQUARES

```
N:1721   MULTIPLE R:0.621   SQUARED MULTIPLE R:0.385
ADJUSTED SQUARED MULTIPLE R:0.382   STANDARD ERROR OF ESTIMATE:12.597
ANALYSIS OF VARIANCE
SOURCE      SUM-OF-SQUARES  DF   MEAN-SQUARE  F-RATIO     P
REGRESSION    170162.882      8   21270.360      134.046   0.000
RESIDUAL       271660.173   1712     158.680
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	41.431	2.225	0	0	18.625	<0.001
OBSHOURS	24.191	1.063	0.464	0.864	22.761	<0.001
TOTFORES	0.126	0.011	0.314	0.488	11.554	<0.001
HETEROGE	6.446	0.705	0.186	0.864	9.148	<0.001
BUILTUP	-0.333	0.046	-0.143	0.907	-7.175	<0.001
POP	1.587	0.268	0.156	0.522	5.93	<0.001
PDYSNOW	-0.213	0.037	-0.181	0.366	-5.788	<0.001
PTOTSNOW	0.004	0.001	0.153	0.356	4.821	<0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	1 800	257.21	139.7
RESIDUAL	1 703	3 135	1.841	
TOTAL	1 710	4 936	2.886	

VARIABLE	ESTIMATE	S.E.	T(1703)
CONSTANT	3.8981	0.0274	142.19
OBSHOURS	0.1165	0.0053	22.07
TOTFORES	0.0022	0.0002	13.76
HETEROGE	0.0765	0.008	9.56
POP	0.0068	0.0013	5.19
AGRICULT	0.0008	0.0002	4.33
BUILTUP	-0.0027	0.0006	-4.13
PDYSNOW	-0.0009	0.0003	-3.36

RICHNESS OF BUILDING NESTING SPECIES

ORDINARY LEAST SQUARES

N:1721 MULTIPLE R:0.713 SQUARED MULTIPLE R: 0.508

ADJUSTED SQUARED MULTIPLE R:0.506 STANDARD ERROR OF ESTIMATE: 1.279

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	2891.657	8	361.457	220.801	0.000
RESIDUAL	2802.593	1712	1.637		

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	0.997	0.293	0	0	3.402	0.001
POP	0.463	0.027	0.4	0.529	17.156	<0.001
OBSHOURS	1.014	0.11	0.171	0.834	9.23	<0.001
TMPMEAN	0.029	0.003	0.24	0.4	8.952	<0.001
WATER	-0.012	0.002	-0.154	0.747	-7.87	<0.001
LOGPRKAR	-0.124	0.021	-0.101	0.951	-5.826	<0.001
HETEROGE	0.421	0.085	0.107	0.614	4.959	<0.001
NOFOREST	-0.241	0.066	-0.092	0.459	-3.666	<0.001
PTOTSNOW	0	0	0.068	0.712	3.375	0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	547.7	78.2416	178.97
RESIDUAL	1 703	744.5	0.4372	
TOTAL	1 710	1 292.2	0.7557	

	ESTIMATE	S.E.	T(1703)
CONSTANT	0.9018	0.0633	14.25
POP	0.0448	0.0026	17.2
OBSHOURS	0.0839	0.0105	8.01
TMPMEAN	0.0484	0.0065	7.4
PTOTSNOW	0.0011	0.0002	6.29
PRKAREA	-0.0159	0.0026	-6.09
PDYSNOW	-0.0049	0.0009	-5.67
WATER	-0.0017	0.0003	-5.12

RICHNESS OF CONIFER NESTING SPECIES

ORDINARY LEAST SQUARES

N:1721 MULTIPLE R:0.795 SQUARED MULTIPLE R:0.633
ADJUSTED SQUARED MULTIPLE R:0.631 STANDARD ERROR OF ESTIMATE:5.275
ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	82179.644	6	13696.607	92.165	0.000
RESIDUAL	47699.436	1714	27.829		

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	24.568	1.985	0	0	12.377	<0.001
TOTFORES	0.096	0.005	0.443	0.389	18.872	<0.001
OBSHOURS	7.567	0.447	0.268	0.855	16.911	<0.001
TMPMEAN	-0.192	0.021	-0.336	0.156	-9.077	<0.001
SOILFERT	-0.043	0.011	-0.068	0.685	-3.824	<0.001
POP	-0.4	0.105	-0.072	0.598	-3.819	<0.001
PSNWCOV5	0.003	0.009	0.011	0.247	0.371	0.711

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	2 899	414.1195	450.44
RESIDUAL	1 703	1 566	0.9194	
TOTAL	1 710	4 465	2.6108	

	ESTIMATE	S.E.	T(1703)
CONSTANT	3.278	0.0481	68.12
TOTFORES	0.0033	0.0002	18.89
OBSHOURS	0.1129	0.0068	16.57
TMPMEAN	-0.0783	0.0056	-14.11
HETEROGE	0.0768	0.0095	8.05
PDYSNOW	-0.0015	0.0004	-4.16
SOILFERT	-0.0015	0.0004	-3.86
POP	-0.0054	0.0015	-3.59

RICHNESS OF DECIDUOUS NESTING SPECIES

ORDINARY LEAST SQUARES

```
N: 1721     MULTIPLE R:0.613      SQUARED MULTIPLE R: 0.376
ADJUSTED SQUARED MULTIPLE R:0.373     STANDARD ERROR OF ESTIMATE:5.603
ANALYSIS OF VARIANCE
SOURCE      SUM-OF-SQUARES  DF     MEAN-SQUARE   F-RATIO    P
REGRESSION     32353.371      8     4044.171       128.818    0.000
RESIDUAL       53747.195   1712       31.394
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	25.253	1.03	0	0	24.524	<0.001
OBSHOURS	10.045	0.476	0.437	0.851	21.096	<0.001
PSNWCOV5	-0.071	0.007	-0.3	0.397	-9.918	<0.001
HETEROGE	2.636	0.314	0.173	0.861	8.397	<0.001
WATER	-0.051	0.007	-0.164	0.691	-7.147	<0.001
TOTFORES	0.036	0.005	0.206	0.411	6.9	<0.001
BUILTUP	-0.142	0.021	-0.138	0.908	-6.898	<0.001
POP	0.524	0.12	0.116	0.511	4.356	<0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	769	109.8379	132.02
RESIDUAL	1 703	1 417	0.832	
TOTAL	1 710	2 186	1.2782	

	ESTIMATE	S.E.	T(1703)
CONSTANT	3.3423	0.0258	129.32
OBSHOURS	0.1076	0.0053	20.18
PSNWCOV5	-0.0014	0.0002	-8.93
HETEROGE	0.0657	0.008	8.16
WATER	-0.0013	0.0002	-7.16
TOTFORES	0.0009	0.0001	6.62
BUILTUP	-0.0036	0.0006	-5.77
POP	0.0055	0.0013	4.11

RICHNESS OF GROUND NESTING SPECIES

ORDINARY LEAST SQUARES

N: 1721 MULTIPLE R:0.594 SQUARED MULTIPLE R: 0.352
ADJUSTED SQUARED MULTIPLE R: .349 STANDARD ERROR OF ESTIMATE: 7.602
ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	53832.648	8	6729.081	116.444	0.000
RESIDUAL	98933.587	1712	57.788		

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	9.47	1.254	0	0	7.551	<0.001
OBSHOURS	12.89	0.64	0.421	0.867	20.135	<0.001
POP	1.454	0.151	0.242	0.594	9.61	<0.001
BUILTUP	-0.257	0.028	-0.188	0.883	-9.072	<0.001
TOTFORES	0.06	0.007	0.255	0.404	8.324	<0.001
NOFOREST	-2.822	0.486	-0.208	0.296	-5.807	<0.001
HETEROGE	3.299	0.605	0.162	0.426	5.45	<0.001
NOCOVERC	1.686	0.442	0.138	0.289	3.811	<0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	1 314	187.703	123.67
RESIDUAL	1 703	2 585	1.518	
TOTAL	1 710	3 899	2.28	

	ESTIMATE	S.E.	T(1703)
CONSTANT	2.9359	0.0318	92.23
OBSHOURS	0.1402	0.0072	19.47
POP	0.0173	0.0017	10.25
TOTFORES	0.0014	0.0002	7.58
BUILTUP	-0.0063	0.0009	-7.13
NOFOREST	-0.0726	0.0124	-5.83
HETEROGE	0.0822	0.0156	5.29
NOCOVERC	0.0412	0.0113	3.63

RICHNESS OF SHRUB NESTING SPECIES

ORDINARY LEAST SQUARES

```
N:1721    MULTIPLE R:0.584    SQUARED MULTIPLE R: 0.341
ADJUSTED SQUARED MULTIPLE R:0.338      STANDARD ERROR OF ESTIMATE:1936.600
ANALYSIS OF VARIANCE
SOURCE     SUM-OF-SQUARES  DF      MEAN-SQUARE    F-RATIO   P
REGRESSION    .332822E+10     8      .416027E+09    110.928   0.000
RESIDUAL      .642072E+10  1712       3750418.140
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	1 293.354	362.258	0	0	3.57	<0.001
OBSHOURS	3 032.473	164.489	0.392	0.852	18.436	<0.001
POP	313.878	41.617	0.207	0.51	7.542	<0.001
HETEROGE	742.703	108.911	0.145	0.855	6.819	<0.001
WATER	-14.786	2.447	-0.143	0.691	-6.044	<0.001
BUILTUP	-40.776	7.118	-0.118	0.911	-5.729	<0.001
PSNWCOV5	-9.997	2.383	-0.126	0.424	-4.195	<0.001
TOTFORES	6.598	1.82	0.111	0.41	3.625	<0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	396.3	56.6184	122.66
RESIDUAL	1 703	786.1	0.4616	
TOTAL	1 710	1 182.4	0.6915	

	ESTIMATE	S.E.	T(1703)
CONSTANT	2.8618	0.0249	115.02
OBSHOURS	0.0862	0.0051	16.78
WATER	-0.0018	0.0002	-9.61
POP	0.0098	0.0013	7.58
HETEROGE	0.0561	0.0078	7.24
PSNWCOV5	-0.0007	0.0001	-4.83
BUILTUP	-0.0022	0.0006	-3.9
TOTFORES	0.0005	0.0001	3.53

RICHNESS OF SNAG NESTING SPECIES

ORDINARY LEAST SQUARES

N:1721 MULTIPLE R:0.556 SQUARED MULTIPLE R:0.309
ADJUSTED SQUARED MULTIPLE R:0.306 STANDARD ERROR OF ESTIMATE:11.825
ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	106950.345	8	13368.793	95.601	0.000
RESIDUAL	239405.284	1712	139.840		

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	23.482	2.12	0	0	11.077	<0.001
OBSHOURS	18.753	0.988	0.406	0.881	18.984	<0.001
PSNWCOV5	-0.143	0.015	-0.303	0.4	-9.547	<0.001
WATER	-0.125	0.014	-0.203	0.831	-9.207	<0.001
BUILTUP	-0.326	0.043	-0.158	0.922	-7.547	<0.001
PTOTSNOW	0.005	0.001	0.21	0.328	6.002	<0.001
HETEROGE	3.691	0.654	0.121	0.883	5.64	<0.001
TOTFORES	0.056	0.01	0.157	0.516	5.623	<0.001

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	291.9	41.6965	99.26
RESIDUAL	1 703	715.4	0.4201	
TOTAL	1 710	1 007.2	0.589	

	ESTIMATE	S.E.	T(1703)
CONSTANT	2.1871	0.0316	69.12
OBSHOURS	0.1179	0.0066	17.97
WATER	-0.0023	0.0002	-10.21
PSNWCOV5	-0.0021	0.0002	-9.41
HETEROGE	0.0611	0.01	6.14
BUILTUP	-0.0044	0.0008	-5.52
PTOTSNOW	0.0004	8.54E-05	5.17
TOTFORES	0.0008	0.0001	5.15

LONG DISTANCE MIGRANT RICHNESS

ORDINARY LEAST SQUARES

```
N:1721    MULTIPLE R:0.192    SQUARED MULTIPLE R:0.037
ADJUSTED SQUARED MULTIPLE R:0.032     STANDARD ERROR OF ESTIMATE:8.144
ANALYSIS OF VARIANCE
SOURCE     SUM-OF-SQUARES      DF     MEAN-SQUARE    F-RATIO   P
REGRESSION     4355.021          8       544.378        8.207    0.000
RESIDUAL      113554.623       1712    66.329
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	25.409	2.28	0	0	11.146	<0.001
TOTFORES	0.048	0.011	0.232	0.206	4.435	<0.001
AGRICULT	0.04	0.01	0.188	0.273	4.15	<0.001
PDYSNOW	-0.067	0.017	-0.11	0.717	-3.921	<0.001
POP	-0.505	0.174	-0.096	0.515	-2.897	0.004
HETEROGE	1.508	0.553	0.084	0.586	2.726	0.006
OBSHOURS	1.615	0.696	0.06	0.841	2.319	0.02
TMPMEAN	-0.056	0.024	-0.102	0.291	-2.316	0.021

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	837	119.5208	137.09
RESIDUAL	1 703	1 485	0.8719	
TOTAL	1 710	2 321	1.3576	

	ESTIMATE	S.E.	T(1703)
CONSTANT	2.9019	0.0311	93.45
TOTFORES	0.0033	0.0002	18.67
OBSHOURS	0.1021	0.0059	17.22
HETEROGE	0.074	0.009	8.22
AGRICULT	0.0011	0.0002	5.55
PDYSNOW	-0.0023	0.0005	-4.97
PTOTSNOW	0.0004	0.0001	4.23
POP	0.0037	0.0014	2.63

RESIDENT/SHORT DISTANCE MIGRANT RICHNESS

```
ORDINARY LEAST SQUARES
N:1721   MULTIPLE R:0.187   SQUARED MULTIPLE R:0.035
ADJUSTED SQUARED MULTIPLE R:0.030   STANDARD ERROR OF ESTIMATE:13.657
ANALYSIS OF VARIANCE
SOURCE      SUM-OF-SQUARES   DF    MEAN-SQUARE   F-RATIO   P
REGRESSION    11512.812       8     1439.102       7.716   0.000
RESIDUAL     319307.163    1712      186.511
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	52.699	3.552	0	0	14.834	<0.001
PDYSNOW	-0.114	0.029	-0.112	0.715	-3.988	<0.001
HETEROGE	3.528	0.914	0.118	0.603	3.86	<0.001
NOFOREST	-2.824	0.735	-0.141	0.418	-3.844	<0.001
WATER	-0.055	0.017	-0.091	0.672	-3.144	0.002
BUILTUP	-0.139	0.05	-0.069	0.911	-2.766	0.006
POP	-0.783	0.298	-0.089	0.496	-2.631	0.009
TMPMEAN	-0.066	0.04	-0.072	0.3	-1.67	0.095

GENERALISED LINEAR MODEL
(Poisson-distributed error term, log link function)

	D.F.	DEVIANCE	MEAN DEVIANCE	DEVIANCE RATIO
REGRESSION	7	1 172	167.437	132.37
RESIDUAL	1 703	2 154	1.265	
TOTAL	1 710	3 326	1.945	

VARIABLE	ESTIMATE	S.E.	T(1703)
CONSTANT	3.4651	0.0234	147.8
OBSHOURS	0.1259	0.0055	22.81
HETEROGE	0.0964	0.0101	9.54
TOTFORES	0.001	0.0001	7.06
BUILTUP	-0.0039	0.0007	-5.95
POP	0.0075	0.0014	5.34
WATER	-0.001	0.0002	-4.91
NOFOREST	-0.0273	0.008	-3.43

APPENDIX C. Ordinary least squares multiple polynomial regression models relating the species richness variables to characteristics of the environment. Predictors variables were added into the models based on the combined F-values of all the polynomial terms. In the following tables the predictors are presented in the order that they appeared in the data file. Abreviations used for the predictor variables in the text are defined below (also see Methods, Table II-1).

AGRICULT= Agricultural land area
BUILTUP= Built-up area
HETEROGE= Heterogeneity
NOCOVERC= Number of land cover classes
NOFOREST= Number of forest classes
OBSHOURS= ln(Observer hours)
POP= ln(Human population)
PRKAREA= ln(Park area)
SOILFERT= Soil fertility
TOTFORES= Total forest cover
TMPMEAN= Mean annual temperature
WATER= Surface water area

TOTAL AVIAN SPECIES RICHNESS

```
POLYNOMIAL ORDINARY LEAST SQUARES
N:1721   MULTIPLE R:0.626   SQUARED MULTIPLE R:0.392
ADJUSTED SQUARED MULTIPLE R: 0.388   STANDARD ERROR OF ESTIMATE:12.537
ANALYSIS OF VARIANCE
SOURCE      SUM-OF-SQUARES   DF   MEAN-SQUARE   F-RATIO      P
REGRESSION    173349.547     12    14445.796     91.903    0.000
RESIDUAL      268473.508   1708      157.186


VARIABLE       COEFFICIENT  STDERROR   STDCOEF  TOLERANCE         T  P(2TAIL)
------------------------------------------------------------------------------
CONSTANT             3.040     6.513     0.000      0.000     0.467    0.641
OBSHOURS            23.022     3.120     1.017      0.019     7.378   <0.001
(OBSHOURS)^2        -1.575     0.392    -0.553      0.019    -4.014   <0.001
POP                  2.375     0.288     0.536      0.084     8.240   <0.001
(POP)^2             -0.215     0.033    -0.435      0.079    -6.464   <0.001
TOTFORES             0.522     0.103     1.303      0.005     5.057   <0.001
(TOTFORES)^2        -0.008     0.002    -2.085      0.001    -3.389    0.001
(TOTFORES)^3         0.000     0.000     1.175      0.002     3.016    0.003
NOCOVERC             7.152     2.213     0.344      0.031     3.232    0.001
(NOCOVERC)^2        -0.721     0.435    -0.169      0.034    -1.658    0.098
NOFOREST             6.776     2.976     0.293      0.021     2.277    0.023
(NOFOREST)^2        -6.770     2.118    -0.814      0.005    -3.196    0.001
(NOFOREST)^3         1.278     0.490     0.419      0.014     2.608    0.009
```

RESIDENT/SHORT DISTANCE MIGRANT RICHNESS

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721      MULTIPLE R: 0.627      SQUARED MULTIPLE R: 0.393
ADJUSTED SQUARED MULTIPLE R: 0.390   STANDARD ERROR OF ESTIMATE: 3.793
ANALYSIS OF VARIANCE
SOURCE        SUM-OF-SQUARES    DF    MEAN-SQUARE   F-RATIO    P
REGRESSION     15945.995        10      1594.599    110.830   0.000
RESIDUAL        24603.145      1710        14.388
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	11.192	1.866	0.000	0.000	5.996	<0.001
OBSHRS	16.138	2.198	1.022	0.018	7.343	<0.001
(OBSHRS)^2	-2.493	0.636	-0.545	0.018	-3.916	<0.001
POP	1.171	0.236	0.379	0.061	4.969	<0.001
(POP)^2	-0.227	0.066	-0.286	0.051	-3.444	0.001
WATER	0.049	0.013	0.234	0.098	3.888	<0.001
(WATER)^2	-0.001	0.000	-0.421	0.102	-7.156	<0.001
AGRICULT	0.075	0.011	0.605	0.041	6.538	<0.001
(AGRICULT)^2	-0.001	0.000	-0.766	0.046	-8.731	<0.001
BUILTUP	-0.025	0.048	-0.036	0.078	-0.528	0.598
(BUILTUP)^2	-0.001	0.001	-0.082	0.097	-1.362	0.173

LONG DISTANCE MIGRANT RICHNESS

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721        MULTIPLE R: 0.620        SQUARED MULTIPLE R: 0.385
 ADJUSTED SQUARED MULTIPLE R:  0.380    STANDARD ERROR OF ESTIMATE: 19.546
ANALYSIS OF VARIANCE
SOURCE            SUM-OF-SQUARES      DF    MEAN-SQUARE    F-RATIO     P
REGRESSION           407696.078        14      29121.148     76.224    0.000
RESIDUAL             651768.738      1706    382.045
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	-17.723	33.064	0.000	0.000	-0.536	0.592
OBSHRS	89.906	56.103	1.114	0.001	1.603	0.109
(OBSHRS)^2	-28.840	31.436	-1.234	0.000	-0.917	0.359
(OBSHRS)^3	4.374	5.701	0.513	0.001	0.767	0.443
POP	5.642	1.138	0.357	0.069	4.958	<0.001
(POP)^2	-1.202	0.303	-0.297	0.065	-3.972	<0.001
WATER	0.721	0.168	0.667	0.015	4.302	<0.001
(WATER)^2	-0.016	0.005	-1.216	0.003	-3.332	0.001
(WATER)^3	0.000	0.000	0.583	0.006	2.373	0.018
TOTFORES	1.183	0.189	1.909	0.004	6.245	<0.001
(TOTFORES)^2	-0.018	0.004	-3.078	0.001	-4.133	<0.001
(TOTFORES)^3	0.000	0.000	1.758	0.002	3.729	<0.001
AGRICULT	-0.055	0.170	-0.086	0.005	-0.320	0.749
(AGRICULT)^2	0.004	0.004	0.598	0.001	0.956	0.339
(AGRICULT)^3	0.000	0.000	-0.417	0.002	-1.014	0.311

RICHNESS OF SNAG NESTING SPECIES

POLYNOMIAL ORDINARY LEAST SQUARES

N: 1721 MULTIPLE R: 0.587 SQUARED MULTIPLE R: 0.345

ADJUSTED SQUARED MULTIPLE R: 0.340 STANDARD ERROR OF ESTIMATE: 11.526

ANALYSIS OF VARIANCE

SOURCE	SUM-OF-SQUARES	DF	MEAN-SQUARE	F-RATIO	P
REGRESSION	119320.103	11	10847.282	81.652	0.000
RESIDUAL	227035.526	1709	132.847		

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2 TAIL)
CONSTANT	-53.836	7.455	0.000	0.000	-7.222	<0.001
OBSHRS	38.076	6.685	0.825	0.018	5.696	<0.001
(OBSHRS)^2	-6.492	1.929	-0.486	0.018	-3.365	0.001
SOILFERT	0.539	0.133	0.519	0.023	4.058	<0.001
(SOILFERT)^2	-0.019	0.005	-0.849	0.006	-3.486	0.001
(SOILFERT)^3	0.000	0.000	0.324	0.018	2.200	0.028
WATER	-0.071	0.015	-0.115	0.661	-4.791	<0.001
TOTFORES	0.256	0.076	0.722	0.008	3.386	0.001
(TOTFORES)^2	-0.002	0.002	-0.577	0.001	-1.067	0.286
(TOTFORES)^3	0.000	0.000	0.170	0.003	0.481	0.630
TMPMEAN	1.543	0.168	1.651	0.012	9.183	<0.001
(TMPMEAN)^2	-0.011	0.001	-1.399	0.013	-8.226	<0.001

RICHNESS OF CONIFER NESTING SPECIES

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POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721        MULTIPLE R: 0.806     SQUARED MULTIPLE R: 0.650
ADJUSTED SQUARED MULTIPLE R: 0.647   STANDARD ERROR OF ESTIMATE: 5.160
ANALYSIS OF VARIANCE
SOURCE        SUM-OF-SQUARES    DF    MEAN-SQUARE   F-RATIO    P
REGRESSION      84458.031       14      6032.717    226.587   0.000
RESIDUAL        45421.048     1706        26.624
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEFF	TOLERANCE	T	P(2TAIL)
CONSTANT	-11.262	10.774	0.000	0.000	-1.045	0.296
OBSHRS	28.816	14.784	1.020	0.001	1.949	0.051
(OBSHRS)^2	-10.168	8.299	-1.242	0.000	-1.225	0.221
(OBSHRS)^3	1.442	1.508	0.483	0.001	0.956	0.339
POP	1.613	1.009	0.292	0.006	1.599	0.110
(POP)^2	-1.000	0.549	-0.705	0.001	-1.822	0.069
(POP)^3	0.112	0.073	0.342	0.004	1.548	0.122
PRKAREA	-0.167	0.259	-0.029	0.105	-0.645	0.519
(PRKAREA)^2	0.277	0.095	0.130	0.102	2.902	0.004
TOTFORES	0.206	0.034	0.949	0.008	6.070	<0.001
(TOTFORES)^2	-0.002	0.001	-0.970	0.001	-2.448	0.014
(TOTFORES)^3	0.000	0.000	0.467	0.003	1.813	0.070
TMPMEAN	0.815	0.337	1.424	0.001	2.418	0.016
(TMPMEAN)^2	-0.015	0.006	-3.270	0.000	-2.723	0.007
(TMPMEAN)^3	0.000	0.000	1.530	0.001	2.444	0.015

RICHNESS OF DECIDUOUS NESTING SPECIES

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721   MULTIPLE R: 0.670   SQUARED MULTIPLE R: 0.448
ADJUSTED SQUARED MULTIPLE R: 0.445   STANDARD ERROR OF ESTIMATE: 5.270
ANALYSIS OF VARIANCE
SOURCE      SUM-OF-SQUARES   DF     MEAN-SQUARE   F-RATIO     P
REGRESSION      38607.687     10      3860.769     139.009   0.000
RESIDUAL        47492.879   1710        27.774
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	-24.124	3.326	0.000	0.000	-7.254	<0.001
OBSHRS	20.549	3.057	0.893	0.018	6.722	<0.001
$(OBSHRS)^2$	-3.288	0.884	-0.493	0.018	-3.722	<0.001
WATER	0.107	0.019	0.346	0.084	5.593	<0.001
$(WATER)^2$	-0.002	0.000	-0.489	0.087	-8.024	<0.001
TOTFORES	0.176	0.035	0.994	0.008	5.067	<0.001
$(TOTFORES)^2$	-0.003	0.001	-1.635	0.001	-3.294	0.001
$(TOTFORES)^3$	0.000	0.000	0.988	0.003	3.032	0.002
BUILTUP	-0.073	0.019	-0.071	0.936	-3.811	<0.001
TMPMEAN	1.137	0.071	2.441	0.014	16.048	<0.001
$(TMPMEAN)^2$	-0.008	0.001	-2.054	0.015	-14.109	<0.001

RICHNESS OF SHRUB NESTING SPECIES

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721       MULTIPLE R: 0.570     SQUARED MULTIPLE R: 0.325
ADJUSTED SQUARED MULTIPLE R:  0.323   STANDARD ERROR OF ESTIMATE: 1959.410
ANALYSIS OF VARIANCE
SOURCE            SUM-OF-SQUARES      DF      MEAN-SQUARE     F-RATIO     P
REGRESSION          .317223E+10        7      .453176E+09     118.036    0.000
RESIDUAL             .657670E+10     1713     3839288.298
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	-301.133	962.723	0.000	0.000	-0.313	0.754
OBSHRS	3 607.670	1 134.117	0.466	0.018	3.181	0.001
(OBSHRS)^2	-127.239	328.208	-0.057	0.018	-0.388	0.698
POP	321.226	33.461	0.212	0.807	9.600	<0.001
WATER	-16.701	2.171	-0.161	0.898	-7.693	<0.001
BUILTUP	-22.835	21.691	-0.066	0.100	-1.053	0.293
(BUILTUP)^2	-0.240	0.318	-0.046	0.104	-0.755	0.451
HETEROGE	690.396	107.615	0.134	0.896	6.415	<0.001

RICHNESS OF GROUND NESTING SPECIES

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721      MULTIPLE R: 0.606      SQUARED MULTIPLE R: 0.367
ADJUSTED SQUARED MULTIPLE R:  0.363   STANDARD ERROR OF ESTIMATE: 7.524
ANALYSIS OF VARIANCE
SOURCE            SUM-OF-SQUARES     DF     MEAN-SQUARE    F-RATIO     P
REGRESSION           56064.935       12       4672.078      82.521    0.000
RESIDUAL             96701.300     1708         56.617
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	-2.759	3.909	0.000	0.000	-0.706	0.480
OBSHRS	23.461	4.312	0.766	0.019	5.440	<0.001
$(OBSHRS)^2$	-3.127	1.248	-0.352	0.019	-2.505	0.012
POP	4.025	0.398	0.671	0.084	10.106	<0.001
$(POP)^2$	-0.784	0.106	-0.510	0.079	-7.423	<0.001
TOTFORES	0.317	0.062	1.346	0.005	5.117	<0.001
$(TOTFORES)^2$	-0.005	0.001	-2.439	0.001	-3.885	<0.001
$(TOTFORES)^3$	0.000	0.000	1.308	0.002	3.290	0.001
NOCOVERC	4.487	1.328	0.367	0.031	3.379	0.001
$(NOCOVERC)^2$	-0.376	0.261	-0.150	0.034	-1.442	0.150
NOFOREST	1.149	1.786	0.085	0.021	0.643	0.520
$(NOFOREST)^2$	-2.851	1.271	-0.583	0.005	-2.243	0.025
$(NOFOREST)^3$	0.486	0.294	0.271	0.014	1.653	0.099

RICHNESS OF BUILDING NESTING SPECIES

```
POLYNOMIAL ORDINARY LEAST SQUARES
N: 1721     MULTIPLE R: 0.748     SQUARED MULTIPLE R: 0.559
ADJUSTED SQUARED MULTIPLE R:  0.557    STANDARD ERROR OF ESTIMATE:  1.211
ANALYSIS OF VARIANCE
SOURCE            SUM-OF-SQUARES     DF     MEAN-SQUARE      F-RATIO      P
REGRESSION            3184.529       10       318.453        216.978    0.000
RESIDUAL              2509.721     1710         1.468
```

VARIABLE	COEFFICIENT	STDERROR	STDCOEF	TOLERANCE	T	P(2TAIL)
CONSTANT	-6.403	0.724	0.000	0.000	-8.848	<0.001
OBSHRS	3.507	0.695	0.593	0.019	5.044	<0.001
(OBSHRS)^2	-0.771	0.201	-0.450	0.019	-3.839	<0.001
POP	0.452	0.024	0.390	0.587	18.606	<0.001
(PRKAREA	0.176	0.061	0.144	0.105	2.903	0.004
(PRKAREA)^2	-0.110	0.023	-0.246	0.100	-4.845	<0.001
NOFOREST	0.542	0.230	0.206	0.034	2.360	0.018
(NOFOREST)^2	-0.341	0.192	-0.361	0.006	-1.779	0.075
(NOFOREST)^3	0.061	0.046	0.175	0.014	1.310	0.190
TMPMEAN	0.233	0.016	1.941	0.015	14.715	<0.001
(TMPMEAN)^2	-0.002	0.000	-1.728	0.016	-13.534	<0.001