

Accounting for the Influence of Geographic Location and Spatial Autocorrelation in Environmental Models: A Comparative Analysis Using North American Songbirds

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ABSTRACT. Environmental models are a critical tool for identifying where organisms occur by estimating the relationship among species occurrence and important environmental factors. To date, the overwhelming majority of predictive occurrence models disregard both the impact of spatial autocorrelation (interaction between neighbouring points) as well as the possibility that model relationships may vary depending on geographic location. To address this gap, we measured their impact on five bird species observed during seven years of the North American Breeding Bird Survey. We first built traditional occurrence models (of varying functional complexity) using logistic regressions and generalized additive models (GAMs). We then compared model accuracy and goodness-of-fit to those incorporating spatial autocorrelation (ALOG) and spatial dependence (via geographically weighted regression, GWR). Environmental variables included aspects of land cover, climate, and topography. A residual analysis indicated that spatial autocorrelation persisted within even the most complex traditional models. In contrast, not only did ALOG models incorporate this effect (as indicated by a lack of residual autocorrelation), but also offered better predictive power for some species (+0.118 in the case of the American Crow, relative to the best GAM model). From an information-theoretic perspective, ALOG models were consistent improvements over traditional models. Adoption of GWR models also improved predictive accuracy (ranging from +0.078 for the American Crow and +0.008 for the Purple Finch). However, comparison of their evidence ratios with ALOG models indicated that ALOG models were generally superior. While we were unable to determine why geographic location influenced species' responses to environmental conditions, evidence from generalized estimating equations (GEEs) revealed significant within-route correlation ($\rho = 0.54 \pm 0.26$ SE), and implicated an observer effect. A combination of broad-scale and fine-scale factors were important for predicting occurrence, but we demonstrate that the incorporation of spatial factors offers the potential to measure the spatially explicit outcomes of intra-specific interactions, and regional differences in resource usage. We recommend that these methods be considered, particularly when evidence points to spatially autocorrelated errors or when there are a priori reasons to suspect geographic variability in resource selection.

Keywords: modeling, species distribution, spatial autocorrelation, autologistic regression, non-stationarity, geographically weighted regression, generalized estimating equation, predictive accuracy, birds

1. Introduction

Environmental modelling is intrinsic to the conceptualization and testing of environmental relationships (Guisan and Zimmermann, 2000) as it improves our ability to understand the ways in which different factors influence phenomena of interest (Austin et al., 1990). In particular, they are often used to empirically evaluate the factors that influence species occurrence, and allow us to: make predictions about where species will occur (Austin, 2002); assist in the identification of areas most likely to support a species of interest (Fielding and Haworth, 1995; Venier et al., 1999; Beissinger et al., 2006); or to highlight the potential distribution of invasive species (Gaston,

2003). Furthermore, predictions are becoming increasingly important in the face of global climate change and the subsequent expectation of shifts in species ranges (Peterson and Kluza, 2003; Gaston, 2003). Whether the modelling objective is better understanding of ecological relationships or prediction, the process of habitat selection (or occurrence) by organisms is one that is spatially realized. Given their predictive power, it is not surprising that modelling is so widely used. However, the overwhelming majority of predictive occurrence models ("traditional models") disregard both the impact of spatial autocorrelation (interaction between neighbouring points) as well as the possibility that model relationships may vary depending on geographic location. Given the importance of accurate models for conservation planning and the large influence of autocorrelation and geographic location (to be discussed), this is a knowledge gap that needs to be addressed.

Legendre (1993) wrote an influential paper that raised the issue of spatial autocorrelation in ecological modelling, and advanced ideas later echoed by Fielding and Haworth (1995),

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Elith et al. (2002), and others. The issue of spatial autocorrelation arises from the fact that proximity to neighbouring individuals is frequently an important factor that influences how observational units respond to their environment, mediated through such fundamental phenomena as spacing behaviour, social structure, and competition (Begon et al., 1990). All of these factors, independent of the characteristics of the local habitat, can be expected to play an important role in determining where (and how) individuals occur in the landscape. In terms of the impact on species distribution models, aggregation (or repulsion) resulting from the interactions between neighbouring individuals produces a local pattern of habitat usage that is autocorrelated (Fielding and Haworth, 1995; Elith et al., 2002; Zhang et al., 2005). Statistically, this has the consequence of overestimating the available degrees of freedom and produces overly optimistic confidence intervals (Legendre, 1993). It may even result in biased parameter estimates (Bonham and Reich, 1999). A growing body of evidence from the ecological literature points to the importance of this effect (e.g. Lichstein et al., 2002; Betts et al., 2006) and confirms that it should not be ignored.

Aside from the influence of spatial autocorrelation, model relationships may vary with geographic location, a phenomenon known as non-stationarity (see Foody, 2004; Fortin and Dale, 2005; Jetz et al., 2005). When location is important, we expect traditional methods (that assume average, uniform effects over the entire region of interest) to mask potentially important and informative local variation in responses (Fotheringham et al., 2002). Osborne and Soares-Seoane (2002) also drew attention to this fact following an analysis in which they partitioned their study region and produced models for each sub-region separately. The recent development of geographically weighted regression (GWR) (Fotheringham et al., 2002) affords an opportunity to consider the effects of location in a manner that alleviates the need to artificially delineate regions into sub-units for analysis. Unfortunately, the vast majority of recently published ecological models make exclusive use of traditional global methods. The indiscriminate application of global models (using smoothed, averaged estimates obtained over the entire region) at local scales, can result in predictions that are inaccurate over many (or possibly all) portions of the area (Burrough and McDonnell, 1998; Fotheringham et al., 2002).

The purpose of this study was to expand understanding of the prevalence and importance of spatial autocorrelation and geographic location, and to do so we used five songbird species obtained from the North American Breeding Bird Survey (BBS). We were particularly interested in the potential to improve model fit and predictive accuracy (assessed using ten-fold cross validation), and adopted approaches designed to incorporate these effects. We addressed spatial autocorrelation using an autologistic regression (AUTO), and the effect of location using a geographically weighted regression (GWR). We then compared this model performance to traditional, non-spatial models (logistic regression and generalized additive models). To further understand the mechanism by which model relationships varied with geographic location, we also considered the potential impact of observer-level (within-route) effects

using generalized estimating equation (GEE) models.

The following key questions were addressed: (1) what evidence is there for spatial autocorrelation; (2) what evidence is there for dependence on location; and (3) how does the inclusion of these spatial effects impact goodness-of-fit and predictive accuracy?

2. Methods

We used a small set of species ($n = 5$), monitored over a seven-year period by participants of the BBS, for a subset of routes ($n = 56$) in the boreal hardwood transition zone (boreal conservation region 12). Using a combination of land cover, climate, and elevation data, we produced a series of predictive species occurrence models. Details of the species distribution data, the study area, the candidate predictor variables, and the model specifications are provided below.

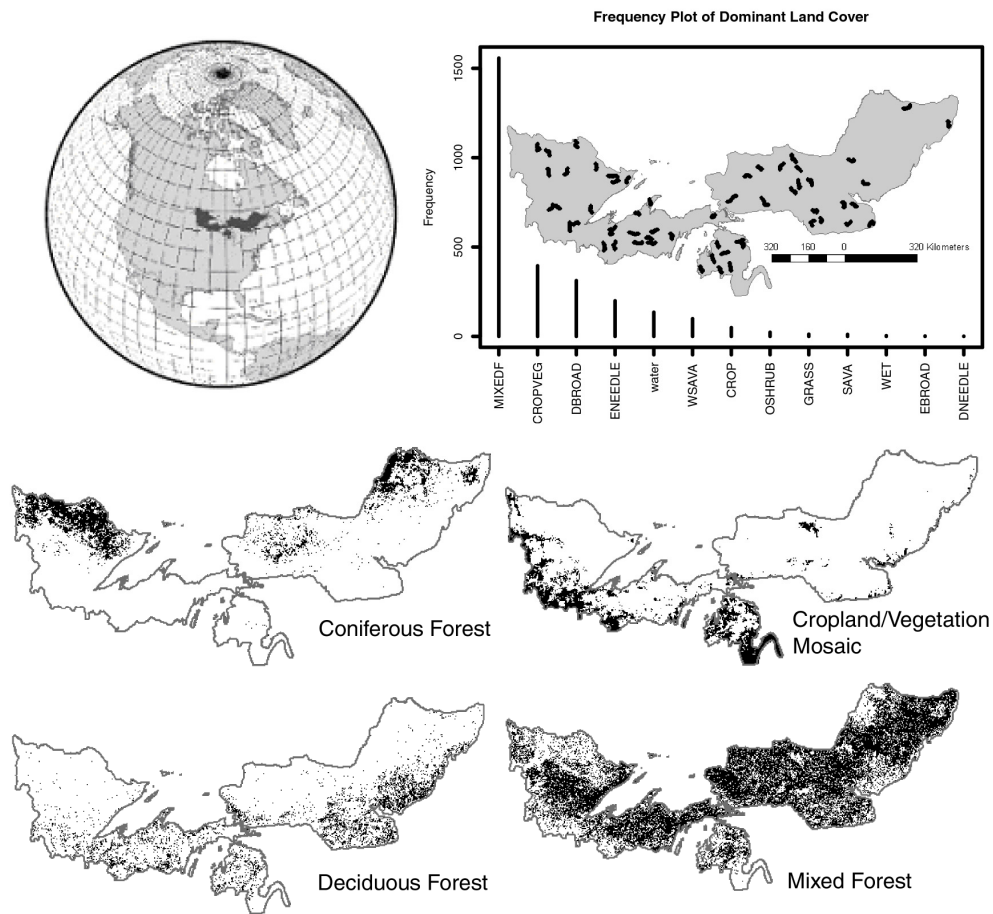
2.1. Species Distribution Data

2.1.1. Selected Species

A subset of North American breeding birds was chosen based partially on the Partners in Flight (PIF) ranking of conservation priority and a minimum prevalence of 2% across all sample locations (see Section 2.1.2). We consulted a specific priority species list (<http://www.bsc-eoc.org/PIF/PIFOntario.html>) compiled for a large portion of the study area (see Section 2.2) and chose four species that exhibited assessment scores (based on the combined consideration of low population size, limited breeding and non-breeding distributions, threats faced during the breeding and non-breeding season, and negative population trends) sufficiently high to place them on the PIF Watch List (see Rich et al., 2004). This included the Blackburnian Warbler *Dendroica fusca*, the Canada Warbler *Wilsonia canadensis*, the Purple Finch *Carpodacus purpureus*, and the Sedge Wren *Cistothorus platensis*. We also examined the American Crow *Corvus brachyrhynchos*, a breeding species that is common and widespread throughout the study area. We felt that this species would serve as a good comparison to the more habitat-specific species due to its status as a true habitat generalist (Freemark and Collins, 1992), and also for its strong tendency to socially interact while foraging, roosting, etc. (Verbeek and Caffrey, 2002).

2.1.2. Data Compilation and Georeferencing

Species occurrence data was obtained from the North American Breeding Bird Survey (BBS), a monitoring project that was initiated in 1966 (Robbins et al., 1986). While primarily intended to detect long-term trends in species abundance, individual volunteer surveys consist of fifty three-minute stop point observations (0.8 km apart) along a defined route, and hence contain valuable information about spatial relationships. For this study, species count data (at the level of the individual stop point) was reclassified as “used” when non-zero counts were noted across any of seven years (from 1997 to 2003). It is possible that defining a sample location as a “presence”



Notes: The histogram presents land cover classifications (see Section 2.3.1 for definitions) for 2799 BBS survey points (located in the inset map).

Figure 1. Geographic location, extent and classified forest cover for the boreal hardwood transition zone (Bird Conservation Region 12, Rich et al., 2004).

point on the basis of a minimum of a single occurrence within the sampling time frame could lump more marginal or rapidly changing habitat with higher quality (more stable) habitat, but we wished to err on the side of including habitat that was potentially usable. We expect that this may inflate the frequency of false-positive prediction error, but this will affect all modeling methods equally, and exert no impact on the model comparisons themselves.

A more important and further-reaching constraint was the inability to identify truly unsuitable (“absence”) locations. In practice, it is difficult to distinguish sites that are unsuitable from those that are vacant due to an observer’s inability to detect a particular species or due to stochastic effects (e.g., otherwise suitable habitat that is only vacant in a given year by chance events). We limited the impact of these effects by pooling data over all available years (seven, in this case) so that we could ensure that sample points defined as “absent” for a given species were, to the best of our knowledge, never utilized within the sampling time frame.

Precisely georeferenced stop points were available for only seven routes in the study area, so we were forced to employ a linear referencing operation in ArcGIS (Environmental Systems Research Institute, 2002) to subdivide individual routes to obtain a larger sample of stop locations. This required a start point, a line indicating the route path, and an assumption that stop points were spaced 0.8 kilometres apart (as specified by the BBS protocol). Due to digitization errors, not all routes could be georeferenced with the same degree of reliability, so routes were only retained (for modelling purposes) if the start points (designated within the BBS dataset) could be located within 0.5 kilometres of each route. This resulted in $n = 56$ routes (2799 stop points). Positional uncertainty remained, however, prompting an evaluation of the remaining discrepancies. Seventy-five points from the precisely georeferenced routes were randomly selected and compared to the location assigned by linear referencing, yielding an average of $1.8 \text{ km} \pm 1.9 \text{ km}$ (SD). This was in close agreement with an average of 1.5 km reported in a previous study (Dobbyn and Couturier, 1998).

Table 1. Candidate Variables Used to Model Species Distributions

Variable	Description	Source
Land Cover:		
LANDCOV	Land cover, grouped into five classes: (1) conifer-dominated forest (CONIFER) (2) cropland-vegetation mosaic (CROPVEG) (3) deciduous-dominated forest (DECID) (4) mixed (conifer-deciduous) forest (MIXED) (5) other (OTHER)	MODIS 2001 land cover classification*
EVIMEAN	Mean Enhanced Vegetation Index (EVI) for a 3x3 neighbourhood	MODIS 16-day EVI**
EVISD	Mean Standard Deviation of the Enhanced Vegetation Index (EVI) for a 3x3 neighbourhood	MODIS 16-day EVI**
Climate:		
DTR	Mean diurnal temperature range (°C)	CRU_2_10 global climate data***
PRECIP	Total annual precipitation (mm)	CRU_2_10 global climate data***
TEMP	Mean temperature (°C)	CRU_2_10 global climate data***
Topography:		
ELEV	Elevation (m)	GTOPO30 global digital elevation model****

*Derived from the MOD12Q1 (1-km resolution) layer incorporating the 17-class land cover classification system defined by the International Geosphere-Biosphere Programme (IGBP) (Friedl et al., 2002).

**Derived from the MOD13A2 (1-km resolution) layer for 25 June, 2004 (Huete et al., 2002).

***Monthly averages (or annual totals, in the case of precipitation) were averaged over the years 1997-2002 at a resolution of 0.5° x 0.5° (Mitchell and Jones, 2005).

****Global digital elevation data at an approximately 1-km resolution (U.S. Geological Survey, 1996).

2.2. Study Area

This region (Figure 1), classified as the boreal hardwood transition zone, was first identified as one of a number of strata in a broad-scale physiographic classification system of North America compiled by Bystrak (1981). This classification was subsequently adopted by Partners in Flight to assist their planning process (Williams and Pashley, 1999). From south to north, this region constitutes a transition zone between mixed hardwood and boreal forest, and is heavily influenced by the presence of the Great Lakes (Ontario Partners in Flight, 2006). A number of political units occur in this area including parts of the American states of Minnesota, Wisconsin, and Michigan, and southern portions of the Canadian provinces of Manitoba, Ontario, and Quebec. The forest communities of this region represent a heterogeneous mix of oaks, maples, birch, and pines in the southern portions of the region, shifting to coniferous species in the more northern, boreal portions (Ontario Partners in Flight, 2006).

2.3. Candidate Predictor Variables

2.3.1. Land Cover Variables

Remote sensing imagery was the source of land cover information for this study. In particular, the Moderate Resolution Imaging Spectroradiometer (MODIS) of the NASA Earth Orbiting System provided a vegetation index image (the Enhanced Vegetation Index, or EVI; see Huete et al., 2002) as well as a supervised land cover classification image (Friedl et al., 2002).

According to Huete et al. (2002), vegetation indices are “spectral transformations of two or more bands designed to enhance the contribution of vegetation properties and allow

reliable spatial and temporal inter-comparisons of terrestrial photosynthetic activity and canopy structural variations.” Furthermore, according to these authors the EVI is particularly sensitive to canopy structural variations, including leaf area index (LAI), canopy type, plant physiognomy, and canopy architecture. It was expected that the EVI could help characterize the structural condition of landscape units, thereby capturing elements of habitat quality. The equation takes the form:

$$EVI = G(\rho_{NIR} - \rho_{red}) / (\rho_{NIR} + C_1\rho_{red} - C_2\rho_{blue} + L) \quad (1)$$

where ρ are atmospherically corrected or partially atmospherically corrected (Rayleigh and ozone absorption) surface reflectances, G is the gain factor, L is the canopy background adjustment that addresses non-linear, differential NIR and red radiant transfer through a canopy, and C_1 , C_2 are the coefficients of the aerosol resistance term, which uses the blue band to correct for aerosol influences in the red band (Huete et al., 2002). The constants G , C_1 , C_2 , and L are empirically determined as 2.5, 6.0, 7.5, and 1.0, respectively (Huete et al., 2002). We used the 1-km² resolution data product, and preliminary analysis suggested that an average EVI based on a 3-km x 3-km neighbourhood (EVIMEAN) was a better predictor than local EVI values. For this reason, the average neighbourhood measure was used in all candidate models (Table 1). An added benefit to a neighbourhood-based approach was that it allowed for the proxy measurement of coarse-scale habitat heterogeneity, estimated using the standard deviation of EVI values in the 3-km x 3-km window (EVISD).

Seventeen global land cover classes (originally developed by the International Geosphere-Biosphere Programme, IGBP)

were defined for the MODIS data at a resolution of 1 km² (Friedl et al., 2002). These classes included: water (water); evergreen needleleaf forest (ENEEDLE); evergreen broadleaf forest (EBROAD); deciduous needleleaf forest (DNEEDLE); deciduous broadleaf forest (DBROAD); mixed forest (MIXEDF); open shrub (OSHRUB); woody savanna (WSAVA); grassland (GRASS); permanent wetland (WETLAND); cropland and cropland/natural vegetation mosaic (CROP); urban and built-up (URBAN). The algorithm used to classify MODIS pixels drew from a database of control sites and a supervised classification method involving a decision tree approach (Friedl et al., 2002). A partial analysis of classification accuracy (for a smaller subset of the 17 IGBP land cover classes), based on fivefold partitioned testing/training data, produced an overall accuracy estimate of 73% (Lotsch et al., 2003). Due to the rarity of most of the IGBP land cover classes within the study area (Figure 1), categories were limited to one of five classes, which were aggregated into a single factor called LANDCOV (Table 1). These classes are: (1) conifer-dominated forest (CONIFER), obtained by combining the original evergreen and deciduous needleleaf forest types; (2) cropland/vegetation mosaic (CROPVEG); (3) deciduous-dominated forest (DECID), obtained by combining the original evergreen and deciduous broadleaf forest types; (4) mixed (conifer-deciduous) forest (MIXEDF); and (5) all other land cover types (OTHER).

2.3.2. Climatic Variables

Climatic measurements were obtained from the global climate data of Mitchell and Jones (2005) for the years 1997 to 2002. Initial candidate variables included: mean monthly temperature (TEMP, in °C); mean monthly diurnal temperature range (DTR, in °C); mean monthly maximum temperature (MAXTEMP, in °C); mean monthly minimum temperature (MINTEMP, in °C); monthly number of wet days (WETDAYS); vapour pressure (VAPOR, in hPa); mean monthly percent cloud cover (CLOUD, in percent); and number of frost days (FROST). Each of the monthly estimates was averaged for the entire year, over all years from 1997 to 2002. Total annual precipitation (PRECIP, in mm) was the final climatic variable used in this study, and like the previous ones, was averaged over all years from 1997 to 2002. Considerations of multicollinearity forced us to retain only three of the previously mentioned variables: DTR, PRECIP, and TEMP (Table 1). However, species distribution studies commonly implicate these particular climatic variables as key drivers (e.g. Venier et al., 1999; H-Acevedo and Currie, 2003).

2.3.3. Topographic Variables

In keeping with the large extent and relatively coarse-scale nature of this study (relative to many other species-distribution modelling studies), we used a 1-km resolution elevation dataset obtained from the GTopo30 global digital elevation model (DEM) of the U.S. Geological Survey's EROS Data Center in Sioux Falls, South Dakota (U.S. Geological Survey, 1996). The grid is approximately 1-km resolution and produced the elevation variable ELEV (in m; Table 1).

2.4. Model Specifications

2.4.1. Logistic Regression (LINLOG and QUADLOG)

All logistic regressions were estimated within the generalized linear model (GLM) framework, with the probability of species occurrence linked to a combination of p linear predictors (X_1, \dots, X_p) via the logistic link function (McCullagh and Nelder, 1999; Collett, 2003):

$$\text{logit}(Y) = \log\left(\frac{P(Y)}{1-P(Y)}\right) = \beta_0 + \sum_{j=1}^p \beta_j X_j \quad (2)$$

Factors considered important determinants of habitat selection (see Section 2.3) and which represent components of the realized niche (Guisan et al., 2002) can be explicitly incorporated into logistic regressions. This approach is very well established, and is traditionally used in predictive species distribution modelling (Guisan and Zimmermann, 2000).

For each species we specified two different logistic regression models: (1) a linear logistic (LINLOG); and (2) a quadratic logistic (QUADLOG). In the first case, all relationships between species occurrences and candidate predictor variables were assumed to be simple linear trends (1 degree of freedom), while in the second case, unimodal relationships were considered (quadratic polynomials, with 2 degrees of freedom).

From a geostatistical point of view, logistic regression models are global interpolators in that they use all available data to make predictions for the whole area of interest (Burrough and McDonnell, 1998). In this respect, the priority of global modelling is to smooth the model relationships to focus on the functional aspects rather than to maximize the fit at individual locations (Burrough and McDonnell, 1998).

2.4.2. Autologistic Regression (ALOG)

Spatial autocorrelation was incorporated by extending the QUADLOG model (Equation 2, with quadratic polynomial terms) to include a spatially lagged autocovariate term (*AUTO*, see Anselin, 2002):

$$\text{logit}(Y) = \log\left(\frac{P(Y)}{1-P(Y)}\right) = \beta_0 + \gamma \text{AUTO} + \sum_{j=1}^p \beta_j X_j \quad (3)$$

The *AUTO* covariate was the product of an $n \times n$ weights matrix (W) and an $n \times 1$ binary vector (y , a 1/0 dummy variable indicating presence or absence at neighbouring points). A simple weighting function was applied to all points:

$$w_{ij} = \begin{cases} 1/8, & \text{if point is one of the eight nearest neighbours} \\ 0, & \text{otherwise} \end{cases} \quad (4)$$

A Gibbs Sampler ($T = 11$ iterations) was used to impute presences in neighbouring, unsampled locations, based on prior knowledge of the relationship between species presence and environmental predictors (see below). The method of Augus-

tin et al. (1996, 1998) was implemented as follows:

1. An ordinary logistic regression (without an autocovariate) was used to produce an initial set of probabilities of occurrence;
2. A random number generator, drawing from a Bernoulli distribution, was used to impute presences for unsampled grid locations;
3. The logistic regression was recomputed, this time with the autocovariate term included;
4. The random number generator was re-applied to impute presences for unsampled grid locations;
5. A Gibb's Sampler was applied, with unsampled points chosen at random (one at a time), the autocovariate recalculated, the conditional probability of occurrence recomputed, and a new random number generator applied to that point. With each iteration of the Gibb's Sampler, the probabilities of occurrence at any given point are progressively updated (given the conditional dependence on the neighbours), ultimately resulting in a model of the joint distribution of all grid points (Augustin et al., 1998).

2.4.3. Generalized Additive Models (GAM)

GAM logistic models are analogous to those estimated by the GLM approach, in the sense that parameters are additive and the response constrained to vary between 0 and 1, but differ by utilizing more generalized smoothing functions to represent the relationship between the j predictor(s) and the response variable (Hastie and Tibshirani, 1990):

$$\text{logit}(Y) = \log\left(\frac{P(Y)}{1-P(Y)}\right) = \beta_0 + \sum_{j=1}^p \beta_j(X_j) \quad (5)$$

The GAM approach has attracted substantial attention and is the subject of a number of reviews in the literature (Guisan and Zimmermann, 2000; Guisan et al., 2002; Segurado and Araujo, 2004; Elith et al., 2006).

For each species, we specified two different GAM models: (1) a model with the same degrees of freedom allocated to the smoothing functions as used in the QUADLOG polynomial logistic regressions (GAM1); and (2) a model with five degrees of freedom allocated to all smoothing functions (GAM2). By keeping the number of degrees of freedom constant, the GAM1 specification permitted the GAM and GLM methods to be directly compared, while the GAM2 specification allowed for the accommodation of more complex responses (e.g. bimodality). It should be noted that spatially, GAM models are like logistic regressions in that all observations within the region of interest are used to estimate model relationships.

2.4.4. Generalized Estimating Equations (GEE)

The GEE approach extends the GLM by allowing for the incorporation of correlated responses (Halekoh et al., 2006; Kleinbaum and Klein, 2002). Such correlation can arise when

repeated measures of the same observational unit are made or observations are grouped within clusters. The consequence of this "within-cluster" correlation is for responses within those clusters to be non-independent, and the estimation of a conventional GLM can result in parameters that are biased or that have overly narrow (overly optimistic) confidence intervals. The logistic model for correlated data looks identical to the ordinary logistic regression model (Equation 2), with the crucial difference that a working correlation structure is specified for describing how the within-cluster responses are related to each other (Kleinbaum and Klein, 2002). Another important difference between the GLM and GEE procedures is that GEE models are estimated using quasi-likelihood methods (Halekoh et al., 2006) that prevent the calculation of likelihood-based AIC values.

In the case of the BBS data used in this study, each of the individual stop points were clustered within one of fifty-six possible survey routes and an exchangeable correlation structure was employed to capture the correlation in their responses. A single correlation parameter (ρ) was estimated for each species to capture the within-cluster effect of the same set of observers conducting all of the stop points for a given survey route. All GEE models were estimated using the *geepack* package (V1.0-10) of Yan (2002) for the R Statistical Package (Ihaka and Gentleman, 1996).

2.4.5. Geographically Weighted Regression (GWR)

Within the binomial GWR framework, parameters are estimated at each sample location using the local neighbourhood of observations, each of which is differentially weighted as a continuously decaying function of distance from the center (Fotheringham et al., 2002):

$$\text{logit}(Y) = \log\left(\frac{E(Y)}{1-E(Y)}\right) = \beta_0(x, y) + \sum_{j=1}^p \beta_j(x, y)X_j \quad (6)$$

It can be seen that for n samples there will be n parameter estimates, each a function of location (represented by Cartesian x and y coordinates). We estimated these parameters using the code originally implemented in the R Statistical language by C. Brunsdon.

2.5. Variable Selection

The aim of this study was to compare the accuracy and performance of a number of predictive models, so our goal was to not to exhaustively explore alternative model structures but to objectively select a reasonable base specification for comparing each of the methods. To identify this baseline model structure we used all candidate predictor variables, fit quadratic polynomial logistic regressions to all continuous variables (QUADLOG specification), and used an all-combinations approach to select a plausible starting model. The all-combinations model selection procedure was used because it avoided the potential vagaries of stepwise model selection. For instance,

an important criticism of stepwise model selection is that important combinations of variables can escape consideration due to prematurely discarding key variables in earlier model selection steps. We found that the all-combinations approach was a practical and robust way to produce this reduced set of variables, provided that we confined variable selection to the logistic regression algorithm. This was a result of the computational demands of all-combinations algorithms. Interactions were not tested.

We used the simple (but objective) rule of choosing the final set of predictor variables that resulted in the QUADLOG regression with the lowest AIC value, and recognized that: (1) it is the relative difference in AIC values that is important, not the absolute values, and (2) some alternative specifications of predictor variables resulted in models that were virtually indistinguishable in terms of relative AIC differences. The final set of predictor variables defined the base specification used to build all subsequent distribution models. In this way, we were able to eliminate variability attributable to differences in model selection procedures and to focus on the head-to-head performance of each of the methods. We advise practitioners who are applying one of the modelling methods in isolation and who have recourse to sufficient time and computational resources to consider the use of bootstrapping to assess the relative importance of predictor variables (Harrell, 2001) or calculate model-averaged estimates for each parameter (Burnham and Anderson, 2002).

Implicit in all starting specifications was an assumption of a potentially symmetric unimodal response to environmental gradients, i.e., some optimum range of conditions in which the probability of habitat usage is maximal, outside of which occurrence declines. We had no a priori reasons to implicate multi-modal responses for any of the environmental gradients, and as partially pointed out by Austin (2002, 2007), due to the following reasons we could not unambiguously determine alternative functional responses anyway: (1) occurrence and environmental data were too coarse a scale (1-km²); (2) environmental variables (e.g. annual precipitation) were indirect (GIS-based) measures of environmental conditions that would, at best, be proxies for direct factors (e.g. moisture availability); (3) model relationships were defined empirically (data-derived); (4) we did not sample the entire environmental gradient for each of the species, i.e. over their entire North American breeding range. Keeping these limitations in mind, we did accommodate the possibility of multimodal or skewed unimodal responses through the estimation of the GAM2 models (Section 2.4.3).

2.6. Assessment of Model Fit and Autocorrelation

As all model predictions were probabilities of occurrence at individual locations, this introduced a threshold dependency in deciding the cutoff point for determining whether test points should be expected to contain an occurrence for that species (for a discussion see Fielding and Bell, 1997). Predictive accuracy, therefore, was assessed using the area under the receiver operating characteristic curve (ROC curve, see Zweig and

Campbell, 1993; Fielding and Bell, 1997), which avoids the threshold problem by integrating across all combinations of possible thresholds. The area under the curve (AUC) of the ROC curve represents the proportion of cases in which the model predictions are consistent with the observed test points (i.e., where model predictions are higher for presence points than absence points), with a value of 0.50 indicating a model no more capable of predicting occurrence/absence than random chance. As pointed out by Elith, et al. (2006), values less than 0.50 indicate models which actually perform poorer than random prediction.

Accuracy assessments, based on the same set of data used to train the models, are prone to overfitting the data at hand, resulting in overly optimistic (biased) accuracy values (Harrell, 2001). We corrected the apparent accuracies using the method of Harrell, et al. (1996):

$$\text{Bias-corrected Accuracy} = AAcc - \left(\frac{1}{10} \sum_{i=1}^{10} AAcc - BAcc_i \right) \quad (7)$$

where *AAcc* is the apparent accuracy (derived using the same set of test data used to build the model) and *BAcc* is the bootstrapped accuracy (derived from one of ten sets of randomly selected test data not used during the model building phase).

With the exception of the GEE method, all other modelling procedures were likelihood based, allowing comparisons among them to be made using relative differences in AIC values. Model calibration was evaluated using the Hosmer and Lemeshow statistic (H-L Statistic, Hosmer and Lemeshow, 2000), which compares the expected number of occurrences (via quintile groupings of the predicted probabilities of occurrence) to those observed. We provide the H-L Statistic as a means for comparing model calibration, but as pointed out by Pearce and Ferrier (2000), the primary goal of predictive modelling is normally to discriminate used from unused locations. As this was our goal as well, we stress the results of the accuracy assessments as a measure of the discriminatory power of each of the modelling procedures.

To evaluate how adequately each modelling method accounted for spatial autocorrelation in species response, model residuals were assessed using the Moran's *I* statistic calculated for varying numbers of nearest neighbours using the 'spdep' package (V0.3-12) of Bivand (2006) for the R Statistical Package (Ihaka and Gentleman, 1996):

$$I = (n / \sum_{i=1}^n \sum_{j=1}^n w_{ij}) \cdot \left[\sum_{i=1}^n \sum_{j=1}^n w_{ij} (y_i - \bar{y})(y_j - \bar{y}) \right] / \sum_{i=1}^n (y_i - \bar{y})^2 \quad (8)$$

where w_{ij} is the distance weighting, n is the number of pairs, and y_i and y_j are the values of y at locations i and j .

2.7. Monte Carlo Resample Test for Non-Stationarity

We evaluated the significance of non-stationarity for the GWR model parameters by employing a Monte Carlo resampling procedure. As described by Fotheringham, et al. (2002),

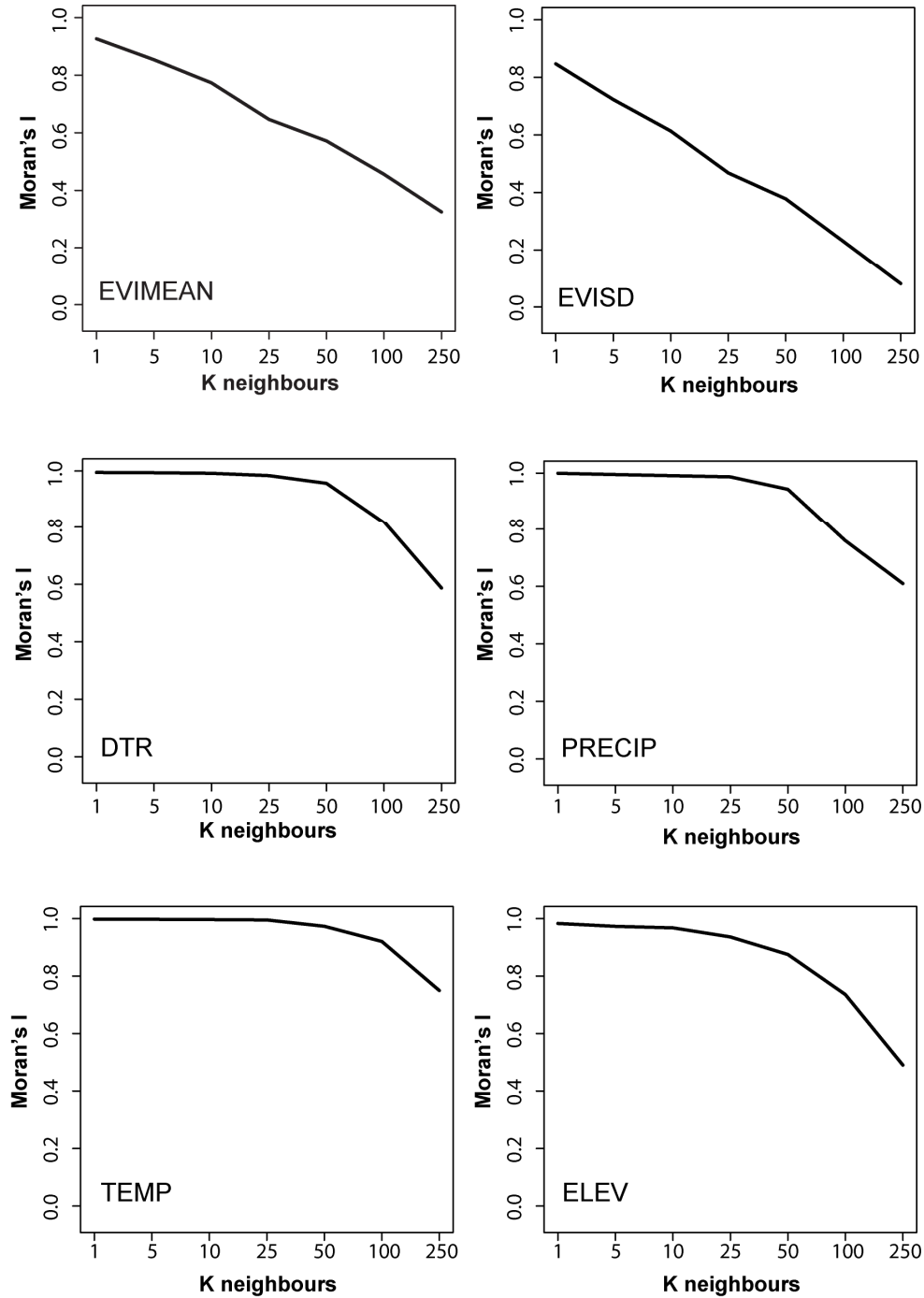


Figure 2. Spatial autocorrelation (measured by Moran's I), over a range of neighbourhood sizes, for six continuous environmental predictor variables: a) mean enhanced vegetation index for a 3-km x 3-km spatial neighbourhood (EVIMEAN); b) standard deviation of enhanced vegetation indices for the same spatial neighbourhood (EVISD); c) average diurnal temperature range (DTR, in °C); d) annual precipitation (PRECIP, in mm); e) average temperature (TEMP, in °C); and f) elevation (ELEV, in m).

the observed spatial variation in parameter estimates should be no different than that expected by chance when the null hypothesis of stationarity is true. To test this null hypothesis we randomly re-allocated the locational coordinates of each sam-

ple point $n = 100$ times, and evaluated the proportion of iterations in which the observed variation in parameter estimates exceeded that of the resample. We considered 5% or fewer cases in which resampled data sets matched or exceeded the

Table 2. Top Five QUADLOG Models Obtained from the All-Combinations Model Selection Procedure, Sorted According to the Lowest AIC Values

	n.p.	AIC	Δ_{AIC}	W_i
AMCR				
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + LANDCOV	16	3452.4	0	0.277
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ²	13	3452.5	0.1	0.264
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	17	3453.2	0.8	0.186
EVIMEAN + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	16	3453.5	1.1	0.160
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + ELEV	11	3454.2	1.8	0.113
BLBW				
EVIMEAN + EVIMEAN ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	15	1620.6	0	0.369
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	17	1620.7	0.1	0.351
EVIMEAN + EVIMEAN ² + EVISD + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	16	1621.7	1.1	0.213
EVIMEAN + EVIMEAN ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + LANDCOV	14	1625.0	4.4	0.041
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + LANDCOV	16	1625.8	5.2	0.027
CAWA				
DTR + DTR ² + PRECIP + TEMP + TEMP ² + ELEV	7	860.2	0	0.381
DTR + DTR ² + PRECIP + TEMP + TEMP ² + ELEV + ELEV ²	8	861.0	0.80	0.255
DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ²	9	862.3	2.1	0.133
PRECIP + TEMP + TEMP ² + ELEV	5	862.4	2.2	0.127
DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	13	862.8	2.6	0.104
PUFI				
DTR + DTR ² + TEMP + TEMP ² + ELEV + LANDCOV	10	1478.1	0	0.348
EVISD + DTR + DTR ² + TEMP + TEMP ² + ELEV + LANDCOV	11	1478.2	0.1	0.331
EVISD + DTR + DTR ² + PRECIP + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	13	1479.4	1.3	0.182
EVISD + EVISD ² + DTR + DTR ² + PRECIP + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	14	1480.7	2.6	0.095
EVIMEAN + EVISD + EVISD ² + DTR + DTR ² + PRECIP + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	15	1482.2	4.1	0.045
SEWR				
EVIMEAN + EVIMEAN ² + EVISD + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	16	652.2	0	0.698
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	17	654.2	2.0	0.257
EVIMEAN + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ² + LANDCOV	16	657.9	5.7	0.040
EVIMEAN + EVIMEAN ² + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ²	13	662.5	10.3	0.004
EVIMEAN + EVISD + EVISD ² + DTR + DTR ² + PRECIP + PRECIP ² + TEMP + TEMP ² + ELEV + ELEV ²	12	665.2	13.0	0.001

Notes: Also presented are the numbers of parameters (n.p.), differences in AIC values (Δ_{AIC}), and Akaike weights (W_i); Δ_{AIC} and W_i are defined relative to the lowest AIC model; See Table 1 for a description of predictor variables.

observed as evidence for rejecting the null hypothesis. It should be noted that this involved repetition of the GWR procedure 100 times for each species, and required approximately twenty-four hours per species on a 1.90 GHz Mobile Intel Pentium computer with 1.0 GB of main memory.

3. Results

3.1. Analysis of Predictor Variables

3.1.1. Spatial Autocorrelation

Preparatory to selecting important predictor variables, we

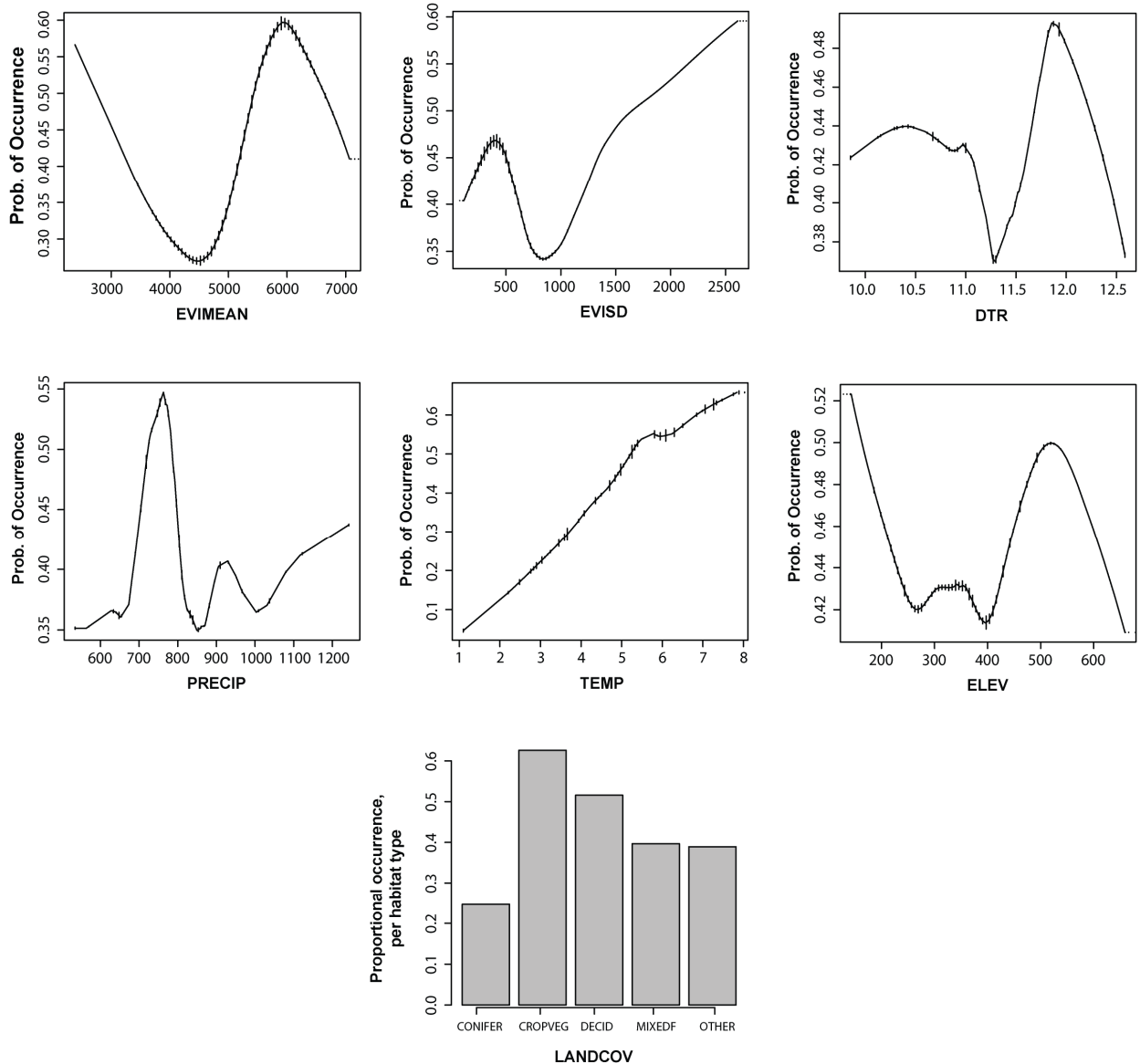


Figure 3a. Exploratory plots of the relationship between occurrence of the American Crow and the environmental predictor variables, using a nonparametric lowest smoother (see Table 1 for definitions).

first investigated the degree to which they were intrinsically autocorrelated. As indicated in Figure 2, all continuous variables showed very high levels of autocorrelation, with Moran's I values in excess of 0.80. The spatial scale varied quite dramatically, with the EVIMEAN and EVISD variables showing a steady decline in autocorrelation with increasing neighbourhood size. The remaining climatic and topographic environmental variables all showed a much lower rate of decay in spatial autocorrelation, with the variable TEMP showing high levels out to the furthest distances of all.

3.1.2. Exploratory Analysis of Effects on Occurrence

Prior to performing the all-combinations model selection

procedure (Section 3.1.3) we constructed exploratory plots of the relationships between species occurrence and the environmental predictor variables (Figures 3a to 3e). Preliminary information conveyed by these plots was for generally unimodal responses. However, there were also instances where responses were multimodal (e.g. American Crow and EVIMEAN) or linear (e.g. American Crow and TEMP). Bar charts for the LANDCOV variable suggested a positive response by the American Crow and Sedge Wren to CROPEVEG-classified landscape units, a positive response by the Blackburnian Warbler to CONIFER-classified units, and a positive response by the Canada Warbler and Purple Finch to MIXEDF-classified units (see Section 2.3).

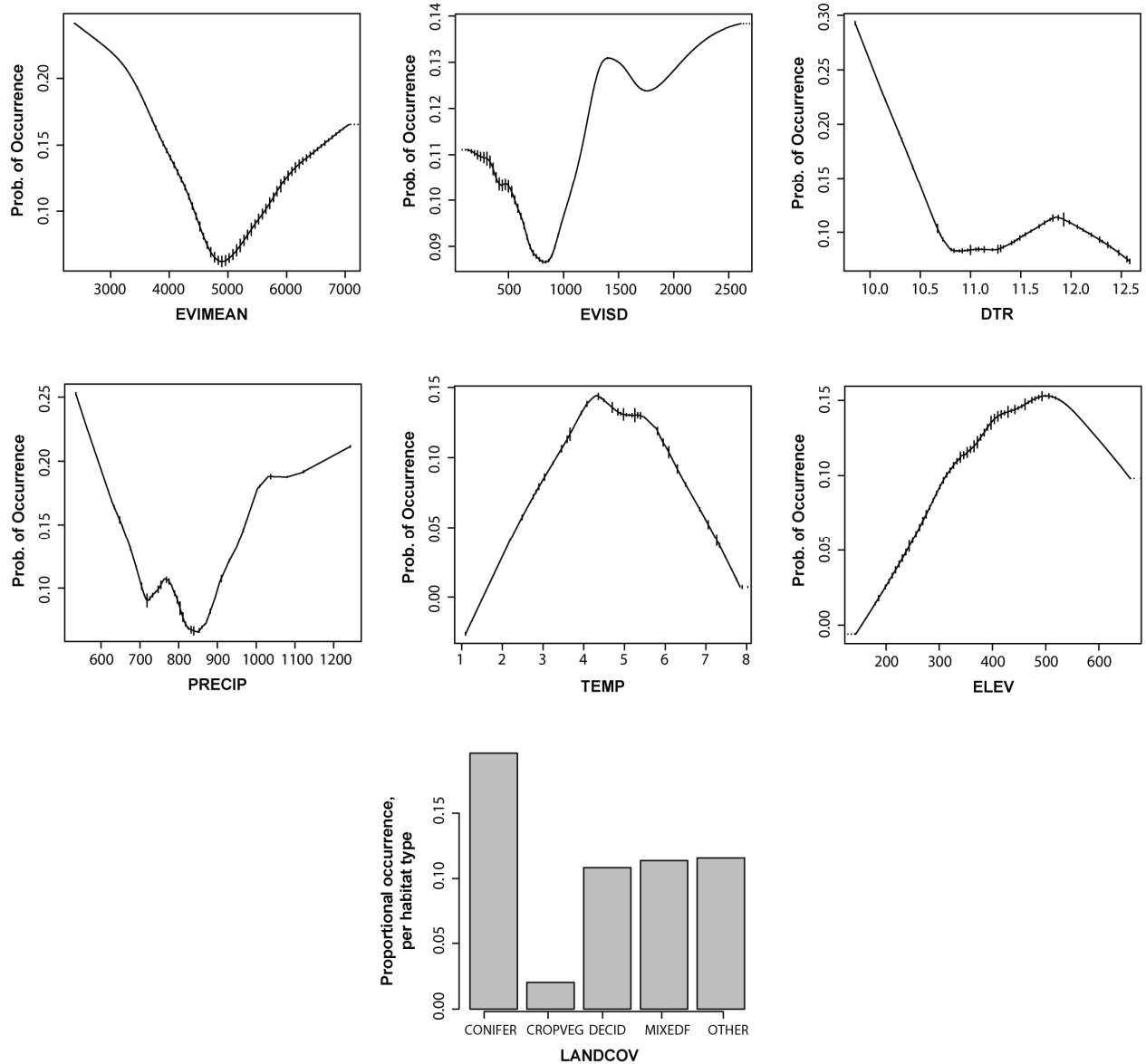


Figure 3b. Exploratory plots of the relationship between occurrence of the Blackburnian Warbler and the environmental predictor variables, using a nonparametric lowess smoother (see Table 1 for definitions).

3.1.3. Identification of Influential Predictors

An all-combinations model selection procedure (see Section 2.5), using QUADLOG models and an AIC-minimization criteria, was used to identify the set of important predictor variables for each species (Table 2). Table 2 presents the five “best” models for each species, ranked according to AIC values. In the case of most species, EVIMEAN and EVISD were retained in the final set of predictor variables, but in quadratic form (e.g. American Crow). In the case of the Canada Warbler and Purple Finch, only climate and elevation (the former), or climate and land cover (the latter) were retained. LANDCOV was retained for all species with the exception of the Canada Warbler.

Table 3. Comparison of Residual Autocorrelation, as Measured by Moran’s *I* (for A Neighbourhood Defined by the Sample Point and Its Two Nearest Neighbours), with Respect to Species and Modelling Method (see Section 2.4)

Method	AMCR*	BLBW*	CAWA*	PUFI*	SEWR*
LINLOG	0.710	0.0672	0.182	0.154	0.099
QUADLOG	0.714	0.0276	0.043	0.120	-0.0018
GAM1	0.696	0.0648	0.063	0.153	0.0072
GAM2	0.602	0.0422	0.038	0.073	-0.0015
GEE	0.714	0.0276	0.043	0.120	-0.0018
ALOG	-0.042	-0.028	-0.013	-0.035	-0.012

*AMCR = American Crow; BLBW = Blackburnian Warbler; CAWA = Canada Warbler; PUFI = Purple Finch; SEWR = Sedge Wren.

3.2. Comparative Analysis of Predictive Models

3.2.1. Impact of Spatial Autocorrelation

Modelling methods differed in their ability to incorporate the effects of spatial autocorrelation, as indicated by their residuals (Table 3). While the most complicated of the non-spatially explicit models (GAM2) had lower residual autocorrelation, it was still unable to eliminate its effect. Therefore, we directly incorporated autocorrelation using a 3-km × 3-km spatial neighbourhood and a succession of ALOG models. Immediately noteworthy was a consistent improvement in model fit relative to non-spatial equivalents (as measured by declines in AIC values; see Table 4). This was especially obvious for the

ALOG model of the American Crow, which had an AIC value several times lower than the non-spatial equivalents. In contrast, predictive accuracy (based on a comparison of ALOG vs. GAM2) was really only improved for the American Crow (+0.118). The remaining species showed a tendency for either no net change in predictive power (Blackburnian Warbler), or a net loss of -0.009, -0.021, -0.008, as in the case of the Canada Warbler, Purple Finch, and Sedge Wren, respectively. The particularly dramatic improvement in predictive accuracy for the ALOG model of the American Crow was consistent with our prior knowledge of the strong autocorrelation in the residuals of its non-spatial models (Figures 4a to 4c). Clearly, the

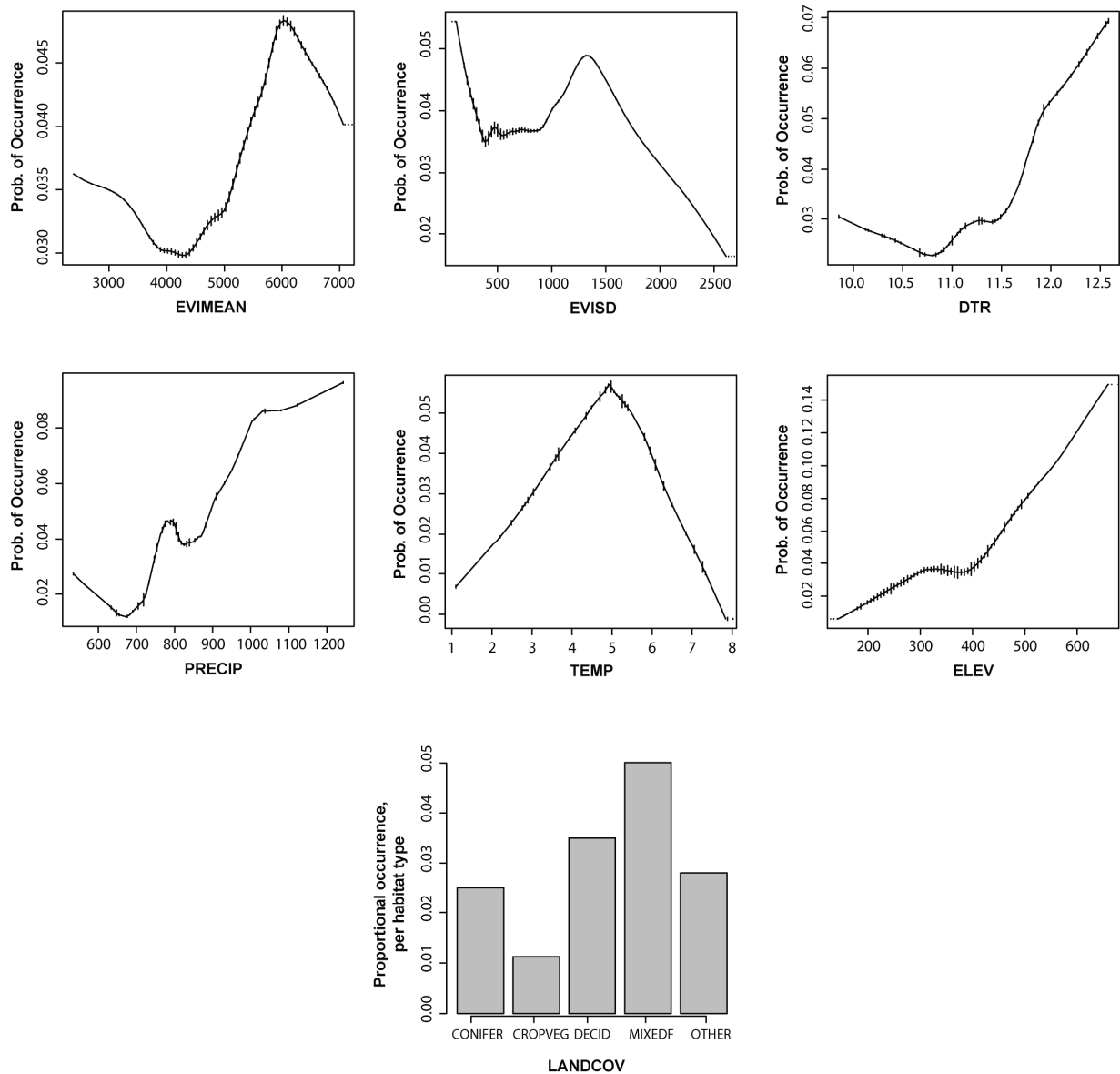


Figure 3c. Exploratory plots of the relationship between occurrence of the Canada Warbler and the environmental predictor variables, using a nonparametric lowess smoother (see Table 1 for definitions).

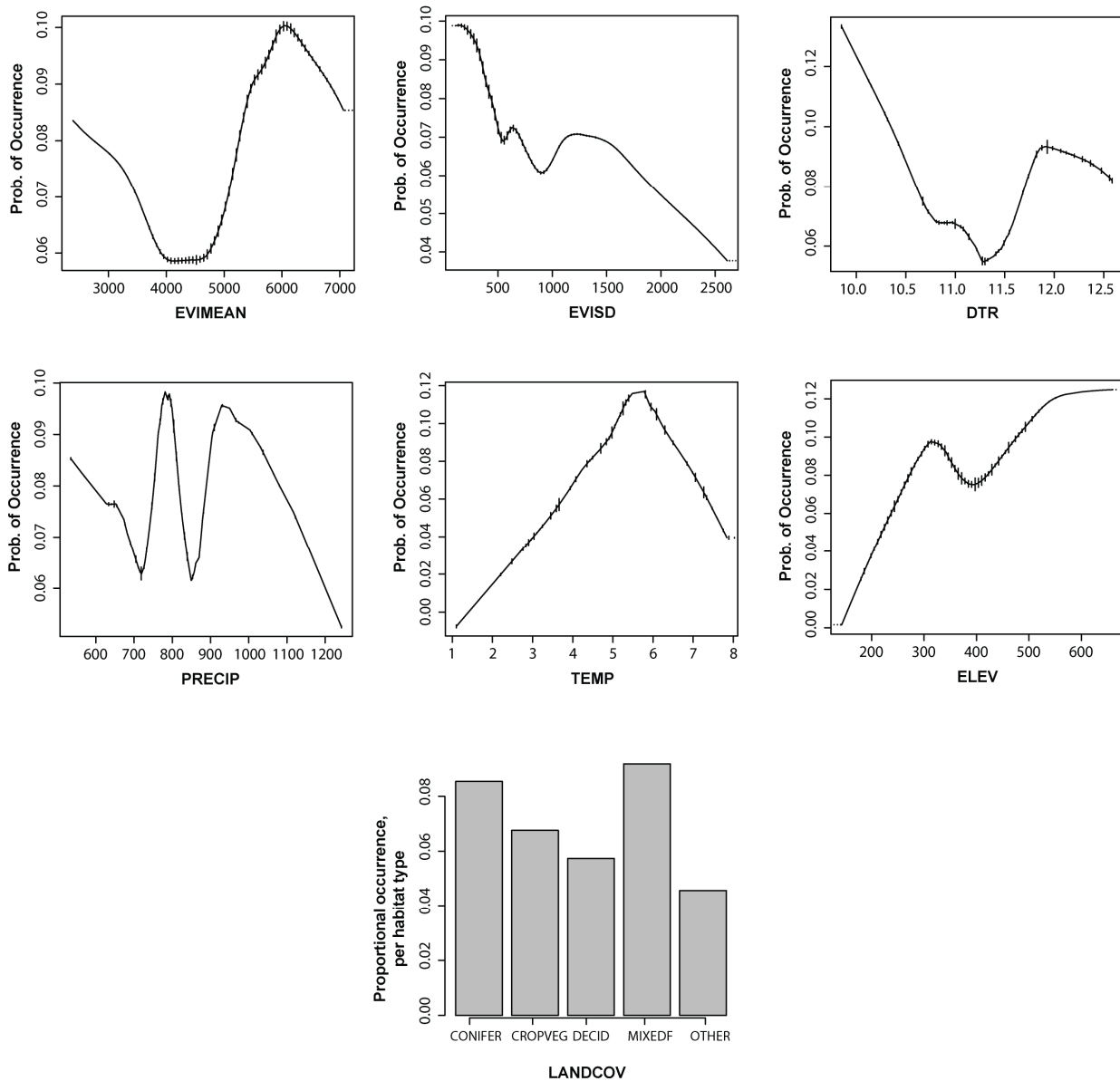


Figure 3d. Exploratory plots of the relationship between occurrence of the Purple Finch and the environmental predictor variables, using a nonparametric loess smoother (see Table 1 for definitions).

American Crow was strongly influenced by proximity to other members of its species.

In summary, while the information-theoretic perspective suggested that ALOG models were consistent improvements over non-spatial models, the assessment of predictive accuracy demonstrated that this was true only for species strongly affected by “endogenous” autocorrelation (sensu Fortin and Dale, 2005), that is, autocorrelation not attributable merely to spatial structure in the environmental predictors themselves.

3.2.2. Impact of Location (Non-Stationarity)

We investigated the influence of location on the species

distribution models through the use of a geographically weighted regression (GWR). Comparison of the AUC values of GWR models with their global, stationary equivalents (Table 4) revealed a tendency for improvements in predictive power. In fact, the GWR models yielded the highest predictive power for four of the five species, with the American Crow standing out as the lone exception. Improvements in predictive accuracy, through the adoption of the GWR approach (relative to the GAM2 non-spatial models), were highest for the American Crow (+0.078), but were also measurable for the Blackburnian Warbler (+0.02), Canada Warbler (+0.027), Purple Finch (+0.008), and Sedge Wren (+0.021).

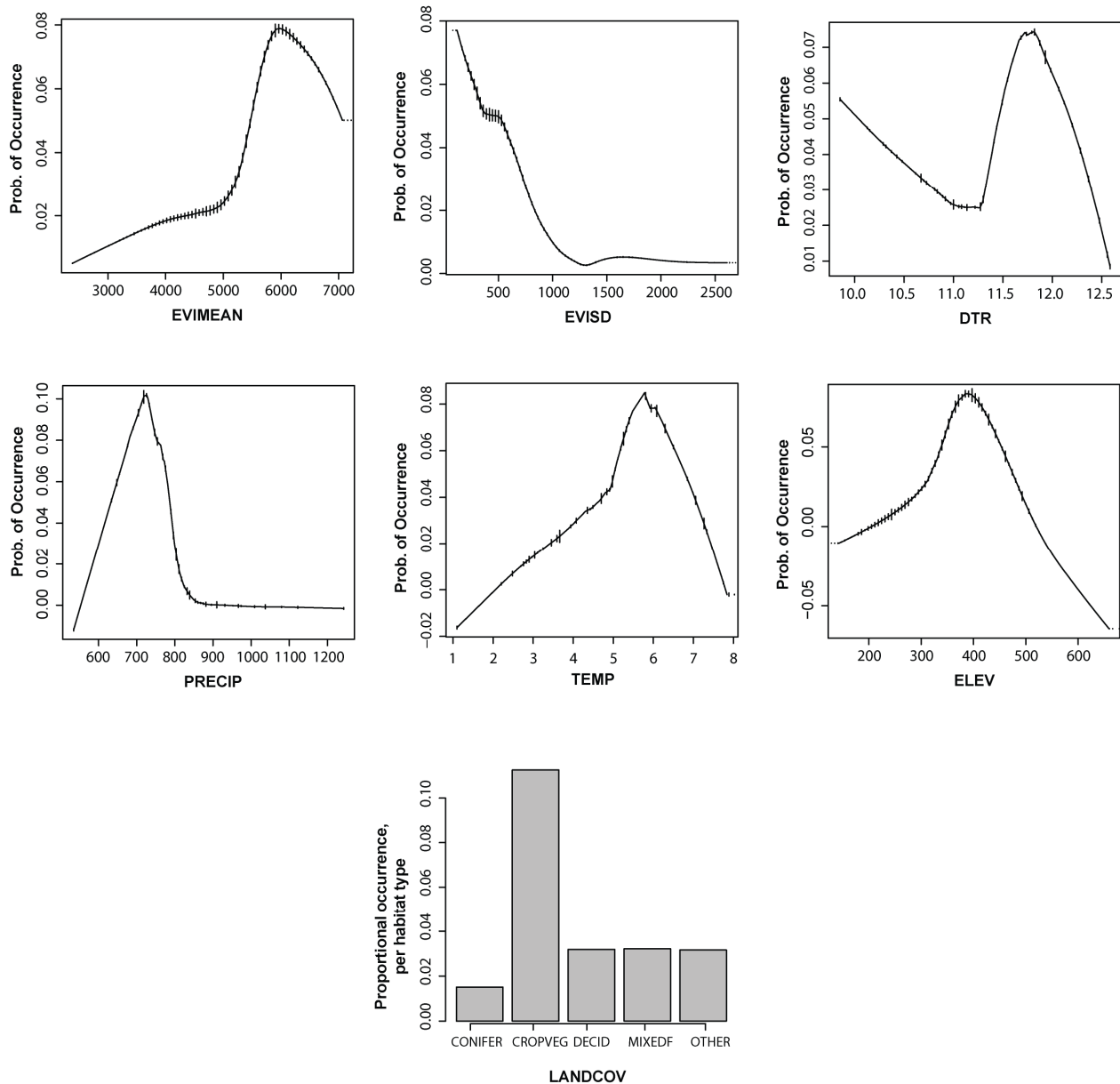


Figure 3e. Exploratory plots of the relationship between occurrence of the Sedge Wren and the environmental predictor variables, using a nonparametric lowess smoother (see Table 1 for definitions).

As measured by AIC values, the GWR models represented large improvements in fit relative to the best of the non-spatial models (i.e. GAM2), but in all cases to a lesser degree than the ALOG equivalents.

We also considered the significance of the non-stationarity using a Monte Carlo resampling procedure (Table 5). For the American Crow, Blackburnian Warbler, Canada Warbler, and Purple Finch, all continuous predictor variables exhibited a significantly high level of spatial variation ($P \leq 0.05$). This contrasted with the findings for the Sedge Wren in which the observed variation in parameter estimates was only significant for DTR, TEMP, and ELEV, but not for PRECIP, EVIMEAN,

or EVISD. With the exception of the American Crow, the categorical variable LANDCOV was not significant for any species in which it was part of the variable set.

3.2.3. Impact of Within-Route (Observer) Effects

As individual survey points were clustered within one of fifty-six possible survey routes, there was a chance that the observer conducting the route may have influenced the probability of detecting and recording species occurrence at each location along the route. This would have introduced a within-route correlation and a breakdown of the independence assumption. To test for this effect, GEE models (using an exchange-

Table 4. Properties of the Statistical Models, including the Akaike's Information Criterion (AIC), Hosmer and Lemeshow Statistic (HL χ^2), and the Area under the Receiver Operating Characteristic Curve (See Section 2.6), by Species and Modelling Method (See Section 2.4)

Method		LINLOG	QUADLOG	GAM1	GAM2	GEE	ALOG***	GWR
AMCR*	AIC	3494.2	3452.4	3366.7	2947	-	1093.7	2295
	HL χ^2	56.6	108.9	19.9	53.9	37.1	16.3	28.4
	AUC**	0.69	0.693	0.72	0.809	0.649	0.927	0.887
BLBW*	AIC	1735.1	1620.6	1614	1524.3	-	1141.8	1483
	HL χ^2	8.68	7.43	18.1	10.2	7.66	15	5.82
	AUC**	0.704	0.756	0.764	0.803	0.754	0.803	0.823
CAWA*	AIC	874.4	860.2	860.3	851	-	744.9	837.2
	HL χ^2	3.3	2.59	2.26	8.1	6.11	10.8	10.1
	AUC**	0.684	0.692	0.703	0.715	0.712	0.706	0.742
PUFI ¹	AIC	1515.2	1478.1	1476	1409.7	-	1205.1	1421
	HL χ^2	12.1	9.8	26.9	11.3	19.5	1.6	7.2
	AUC ²	0.63	0.672	0.673	0.72	0.683	0.699	0.728
SEWR ¹	AIC	836.9	652.2	679.2	610.9	-	483.9	669.9
	HL χ^2	2.8	24.5	10.6	3	18.5	1.1	3.2
	AUC ²	0.815	0.907	0.9	0.917	0.916	0.909	0.938

* AMCR = American Crow; BLBW = Blackburnian Warbler; CAWA = Canada Warbler; PUFI = Purple Finch; SEWR = Sedge Wren.

** Bias-corrected accuracy values, based on 10 sets of bootstrap-resampled test points (see Methods).

*** The autologistic results are presented for $k = 8$ nearest neighbours.

able correlation structure) were estimated for each species and a single correlation parameter (ρ) calculated. The results of the GEE models revealed that only the American Crow exhibited significant ($p < 0.05$) within-route correlation: 0.54 ± 0.26 SE. Values for the remaining species were 0.12 ± 0.37 (Blackburnian Warbler), 0.049 ± 0.11 (Canada Warbler), 0.12 ± 0.13 (Purple Finch), and 0.064 ± 0.35 (Sedge Wren). Consideration of the effect of incorporating within-route correlation (Figure 5) reveals that standard errors were considerably wider for the climatic variables: DTR, PRECIP, and TEMP. There were also changes in the values of the coefficients for EVIMEAN and EVISD. ELEV and LANDCOV were unaffected.

4. Discussions

4.1. Influence of Autocorrelation (Proximity)

Initially, autocorrelation was assessed by examining the pattern of residual error for non-spatial models. Species that tend to show clustered or patchy distributions should be the least adequately modelled by non-spatial methods. Judging from residual autocorrelation, models based purely on environmental variables appeared adequate for four of the five species. This made sense given the fact the environmental variables themselves exhibited high levels of autocorrelation, such that the bulk of proximity effects could be accounted for by the

spatial distribution of the environmental factors alone.

However, even the most complex non-spatial model (i.e. GAM2) was unable to mitigate residual autocorrelation for the American Crow. Major proximity effects played an important role in determining the distribution of this species, independent of environmental factors. Therefore, it made sense that incorporating an autocovariate would eliminate residual autocorrelation, improve model fit, and boost predictive accuracy. From an information-theoretic perspective there was a tendency for all species to benefit from the inclusion of a proximity effect, as indicated by the substantially lowered AIC values for ALOG models.

4.2. Influence of Location (Non-Stationarity)

Location exerted a strong effect on modelled relationships, particularly for the American Crow. This was consistent with the expectation that different factors, possibly combined with regional differences in adaptation, could result in model relationships that vary through space. Evidence for the importance of this effect came from the Monte Carlo significance tests, as well as from the improvements in model fit and predictive accuracy. There were species-specific differences, however, with the greatest improvements in AIC and AUC values realized for the American Crow and Blackburnian Warbler, respectively. In

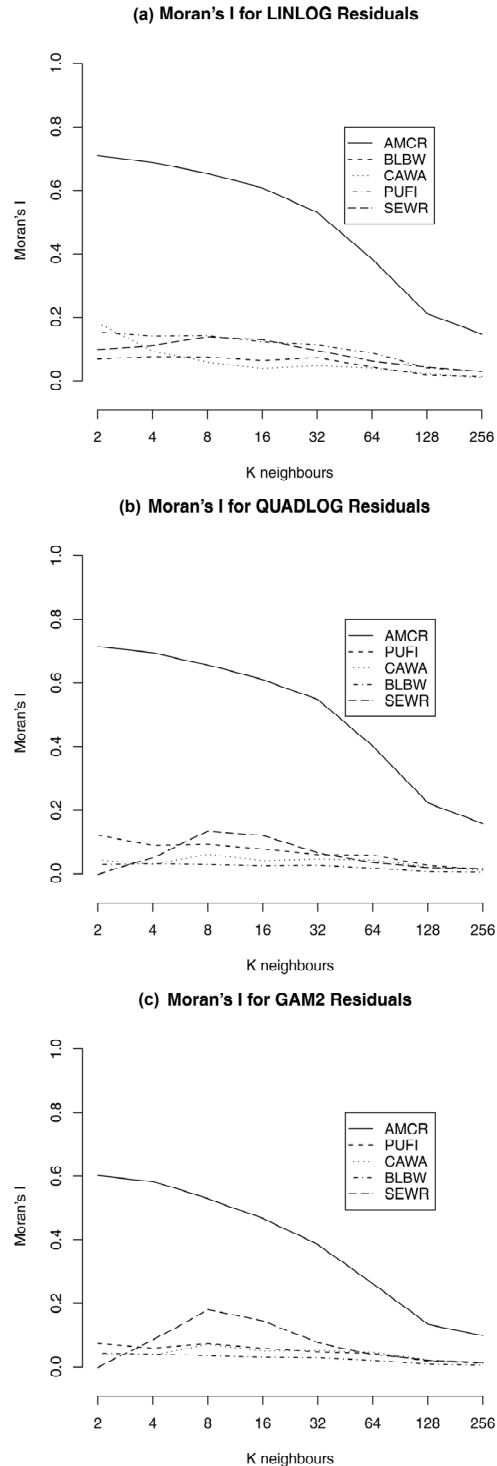
contrast, large-scale spatial variation for the Sedge Wren, based on the Monte Carlo tests, was significant for less than half of the predictor variables (Table 5). This may have been a product of the smaller sample size for this species, but it may also be attributable to its smaller geographical distribution within the study area (estimated at 153,686 km², or about 25% of the total extent, based on a minimum convex polygon enclosing the presence points). Possibly this represents a lower bound of geographical extent for consideration of non-stationarity at the scale of this study.

Table 5. Monte Carlo Tests of the Significance of Non Stationarity in Parameter Estimates for the GWR Statistical Models

Variable	AMCR	BLBW	CAWA	PUFI	SEWR
Land Cover					
LANDCOV*	<0.01	0.06	--	0.21	0.36
EVIMEAN	<0.01	<0.01	--	--	0.60
EVIMEAN ²	<0.01	<0.01	--	--	0.58
EVISD	<0.01	--	--	--	0.86
EVISD ²	<0.01	--	--	--	--
Climate					
DTR	<0.01	<0.01	<0.01	<0.01	<0.05
DTR ²	<0.01	<0.01	<0.01	<0.01	<0.05
PRECIP	<0.01	<0.01	<0.01	--	0.13
PRECIP ²	<0.01	<0.01	--	--	0.13
TEMP	<0.01	<0.01	<0.01	<0.01	0.05
TEMP ²	<0.01	<0.01	<0.01	<0.01	0.05
Topography					
ELEV	<0.01	0.01	<0.01	<0.01	0.01
ELEV ²	<0.01	<0.01	--	--	0.01

* Significance averaged over all indicator variables

What drove spatial non-stationarity? Clearly, spatial variation in model relationships were statistically significant for most variables, that is, greater than expected by chance given the null hypothesis that model relationships were the same everywhere. The geographical arrangement of the responses introduced variation that could not be explained purely by environmental conditions. However, the potential for localized overfitting (discussed later in more detail), or misspecification of the functional form of the relationships due to subsampling of the entire range of conditions (Austin, 2007), is always a risk. In the case of this study, the size of the GWR kernel (512 km) may have coincided with a sufficiently high level of autocorrelation in some of the predictor variables (Figure 2) to have contributed to non-stationarity. By sharing neighbouring positions along each of the environmental gradients, nearby points could lead to models that are purely an artifact of the particular range of conditions sampled by those points. In an example (see Figure 5) provided by Austin (2007), species response to rainfall was steeply linear in one portion of the gradient, but unchanging in a latter portion of the gradient. However, this explanation is unlikely to account for non-stationarity in the less strongly autocorrelated variables (such as EVIMEAN). Further to this point, Fotheringham et al. (2002) implicate three other



Notes: AMCR=American Crow; BLBW=Blackburnian Warbler; CAWA=Canadian Warbler; PUFI=Purple Finch; SEWR=Sedge Wren.

Figure 4. Plot of residual autocorrelation, as measured by Moran's I, with respect to species and modelling method: (a) linear logistic regression (LINLOG), (b) quadratic logistic regression (QUADLOG), and (c) GAM2.

factors capable of driving non-stationarity: (1) spatially-biased sampling error; (2) a process that is genuinely dependent on the location where it is observed; and (3) the presence of unmeasured but influential factors that are capable of accounting for the observed spatial pattern.

In considering the possibility that sampling error was dependent on location, we need to revisit the results of the GEE models. The American Crow exhibited significant within-route correlation, which strongly suggested the influence of an observer effect on the probability of this species being both detected and recorded as present. Of the five species examined, gains in predictive accuracy through adoption of the GWR approach (relative to GAM2 non-spatial models) were also greatest for the American Crow (approximately three-times higher than the next highest species, the Canada Warbler). Taken together, this suggests that an important proportion of the non-stationarity in the American Crow GWR model could be attributed to route-level effects (i.e. the observer).

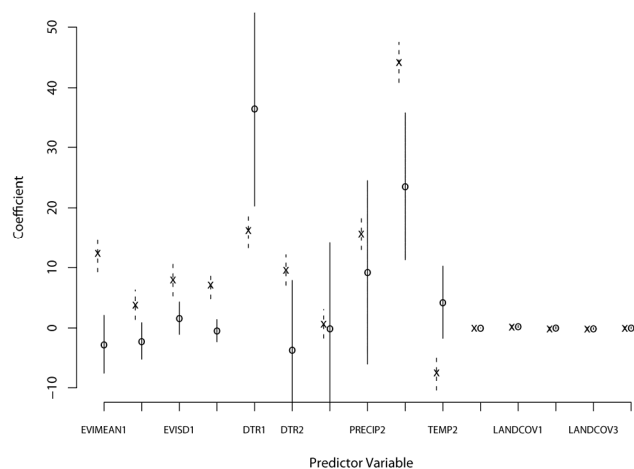
Despite the evidence for observer effects on the detection and recording of American Crows, we still cannot rule out the possibility that the process of habitat selection was not also geographically dependent or that other unknown (or unmeasured factors) were active in different portions of the study area. In the first case, the species is common and widespread and could quite conceivably exhibit localized adaptation to environmental conditions. In the second case, given the coarse-scale nature of the study there may have been finer-scale, unmeasured factors (e.g. food availability) driving geographic variation. We suggest that only a carefully controlled study, conducted at wide spatial extent but fine-scale resolution, could test the relative importance of these factors.

Methods such as GWR, which allow modelled relationships to vary with location, have the potential to capture regional differences in resource selection (as in this study), behaviour, or any other ecological phenomenon of interest. Given its flexibility and power to generate new insights, we feel that this method should receive greater attention from the ecological and modelling community. However, we also concur with Jetz et al. (2005) that general inferences can be difficult to make in an environment where parameter estimates assume a wide range of geographically specific values, and that non-biologically meaningful sources of variation may be captured by GWR regressions. One way to avoid the latter problem may be to apply Monte Carlo significance tests for non-stationarity as done here.

Consideration must also be given to the appropriate scale (neighbourhood size) to search for non-stationarity, which we feel represents an important area of research for GWR applications in species distribution modelling. A priori expectations about the geographical range of local adaptation could help guide the choice of neighbourhood size and may reveal potentially important and informative geographic variation. Alternatively, geographic variation may be attributable to the presence (or absence) of the effects of important predictor variables and may help guide subsequent investigation into new (or possibly overlooked) factors.

4.3. Species-Specific Responses

One interesting aspect of our study was its cross-scale nature: we were able to simultaneously address factors operating at local scales (e.g. dominant forest cover) as well as those operating over much larger spatial scales (e.g. average annual temperature). This can be directly attributed to the geographically wide extent of the individual BBS survey routes (each with fifty individual sample points). While the particular variables retained in each model varied for each species, all showed sensitivity to a mixture of fine-scale (land cover) and broad-scale (climatic and topographic) factors. The goal of our study was to highlight prominent trends, not to rigorously test hypotheses about functional responses to environmental gradients – an unachievable goal given the coarse scale of the study (meaning that all predictor variables were indirect factors) and the fact that we didn't sample the entire range of conditions experienced by each species over its entire range.



Notes: The coefficients and standard errors of individual predictor variables are shown for a traditional model not incorporating within-route effects (QUADLOG, indicated by crossed symbols, broken lines) as well as the GEE model (solid circles and lines); See Table 1 for variable definitions.

Figure 5. GEE model for the American Crow incorporating the effects of within-route correlation.

All five species responded to broad-scale variation in average annual diurnal temperature range, average annual temperature, and elevation, with total annual precipitation only failing to be retained in models for the Purple Finch. Conventional wisdom in biogeography maintains that external, large-scale environmental factors such as temperature (Root, 1988) or other measures of ecosystem productivity (Currie, 1991; Irwin, 1998) are key determinants of broad-scale species distribution. A number of studies provide strong empirical evidence in favour of this notion (e.g. Venier et al., 1999) and demonstrate that useful predictions can be made at biogeographic (or near-biogeographic) scales using this information alone. The findings of our study reinforce this notion in that all five passerine species showed significant relationships with clima-

tic variables. Furthermore, four of the five species are migratory and do not occur within the study area during the winter season, so we expect much of the response to average climatic conditions was likely of the “distal” type described by Austin (2002), in which the integration of climatic conditions over time acts through an indirect chain of events to influence the suitability of particular locations for these species. This effect could ultimately manifest itself by influencing food availability or habitat (Venier et al., 1999).

Despite the importance of climatic conditions, local land cover features (such as dominant forest class) were a significant influence on species occurrence. The modelled relationships were also consistent with previously documented habitat associations, lending confidence to the results. The American Crow, a species known for its preference for a mixture of open fields for foraging and scattered woods for nesting (Godfrey, 1966; Verbeek and Caffrey, 2002), commonly frequents agricultural land during the breeding season (Cadman et al., 1987). This species’ tendency to occur in fragmented agricultural landscape was represented in the distribution model by a positive association with EVISD and the CROPVEG class of LANDCOV.

While models for the Sedge Wren also showed a positive response to the CROPVEG class, they showed a negative response to EVISD. This may have been reflective of the species’ preference for wet meadows, hayfields, and retired croplands, but in areas of evenly distributed woody vegetation used as cover (Godfrey, 1966; Herkert et al., 2001). The negative response to EVISD was consistent with previously published findings for this species to occur in relatively intact (i.e. unfragmented) grassland cover (Bakker et al., 2002; Fletcher and Koford, 2002). While this species is considered transitory, that is, likely to nest in different locations from year to year (Herkert et al., 2001), it appeared to occur in a narrow enough range of landscape types to be predicted with a high degree of accuracy. It may be that aggregating occurrence information over the seven-year period of this study also helped to yield a larger sample of occurrences for this rare species. It is also possible that the coarse scale of the predictions, applied over an area of large spatial extent, may have lessened the impact of year-to-year variation in the location of nesting sites. We expect that attempts to predict occurrences at finer spatial and temporal scales might result in higher false-positive prediction error, that is, a tendency to predict occurrence in suitable landscape units that are, in fact, unoccupied due to stochastic variation in micro-site conditions. Moisture availability, for instance, appears to be a candidate factor that acts in this way (Dechant et al., 1998).

Of the two warblers in this study, the Blackburnian Warbler is known to associate with mature conifer-dominated woodland (Cadman et al., 1987; Morse, 2004), although recent habitat association studies have documented preference for mixedwood forest, depending on scale (Girard et al., 2004; Young et al., 2005). Our study, limited to the 1-km scale of the MODIS land cover classification, detected a preference for the CONIFER-class of LANDCOV (Figure 3b). Subtleties of habitat usage within those landscape units (e.g. choice of individual trees for singing or foraging) were not measured. The

Canada Warbler is known to prefer mixedwood forest (Cadman et al., 1987; Conway, 1999), but we were unable to establish a link between this species and the MIXED-class of LANDCOV. Finally, models for the Purple Finch were most strongly associated with the CONIFER and MIXEDF classes of LANDCOV (Figure 3c), which was consistent with its documented preference for nesting in conifer-dominated or conifer-deciduous mixed forest (Godfrey, 1966; Wootton, 1996; Machtans and Latour, 2003).

One local-scale variable of special interest to us was EVISD, the standard deviation of the enhanced vegetation index (EVI), which we postulated may index landscape fragmentation. The EVISD variable was a largely non-significant factor in all of our models, with the exception of the American Crow (which showed a positive response to this variable) and the Sedge Wren (which showed a negative response). Species considered sensitive to habitat fragmentation or vegetation species composition (e.g. the Blackburnian Warbler and the Canada Warbler) did not show a significant response to EVISD. Given that the finest resolution of EVI values for our MODIS land cover data was 1 kilometre, and the possibility of pixel mixing, it may be that our EVISD measure was too coarse to generally capture this effect. We concur with the recommendation of Kadmon et al. (2003) that data used to test hypotheses be gathered at a finer scale than that for which inferences are to be made, and for this reason speculate that 1-km² land cover data may have been of inadequate resolution. Nevertheless, other unmeasured characteristics of the land cover variables (e.g. vegetation structure) may have acted as important missing components.

4.4. Recommendations

We present evidence that consideration of the effects of autocorrelation and non-stationarity, via spatially autocorrelated or geographically weighted models, can improve model fit and raise predictive accuracy. However, they introduce additional complexities that may limit their general use. For instance, the use of spatially autocorrelated models to make predictions about probability of occurrence in unsampled areas (for purposes of interpolation) requires special simulation of presence in those areas (e.g. via a Markov Chain Monte Carlo approach; see Wu and Huffer, 1997; Augustin et al., 1998). Furthermore, it is our experience that without a priori expectations about the spatial pattern of model relationships, inferences about GWR estimates can also be challenging to make, that is, it can be difficult to determine whether or not the geographic variation is biologically meaningful. As well, use of GWR warrants consideration of the risk of over fitting models that may be less generalizable outside the region of study.

Because of the difficulties previously mentioned we recommend an iterative process for incorporating spatial effects. First, non-spatial models can be estimated and the adequacy of environmental predictor variables determined. Second, autocorrelation in model residuals can then be assessed using a measure such as Moran’s I. Species that exhibit a tendency to be patchily distributed (e.g. the American Crow) should exhibit more poorly fit models, and be of lower accuracy, than less

patchily distributed ones. These species represent good candidates for an autologistic approach. In this study, proximity effects exerted a stronger overall impact on models than location, but for studies occurring over large areas, or for which a priori reasons exist for suspecting geographic differences in model relationships, a GWR approach may be quite helpful. Investigators must still contend with interpretation of those geographic patterns, but GWR can raise new and interesting questions about model relationships or suggest the influence of unknown or unmeasured factors.

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References

- Anselin, L. (2002). Under the hood: issues in the specification and interpretation of spatial regression models, *Agric. Econ.*, 27, 247-267, doi:10.1111/j.1574-0862.2002.tb00120.x.
- Augustin, N.H., Muggleston, M.A., and Buckland, S.T. (1998). The role of simulation in modelling spatially correlated data, *Environmetrics*, 9, 175-196, doi:10.1002/(SICI)1099-095X(199803/04)9:2<175::AID-ENV294>3.0.CO;2-2.
- Austin, M.P., Nicholls, A., and Margules, C. (1990). Measurement of the realized quantitative niche: environmental niches of five eucalyptus trees, *Ecol. Monogr.*, 60, 161-174.
- Austin, M.P. (2002). Spatial prediction of species distribution: an interface between ecological theory and statistical modeling, *Ecol. Model.*, 157, 101-118, doi:10.1016/S0304-3800(02)00205-3.
- Austin, M.P. (2007). Species distribution models and ecological theory: a critical assessment and some possible new approaches, *Ecological Modelling*, 200, 1-19, doi:10.1016/j.ecolmodel.2006.07.005.
- Bakker, K.K., Naugle, D.E., and Higgins, K.F. (2002). Incorporating landscape attributes into models for migratory grassland bird conservation, *Conserv. Biol.*, 16, 1638-1646, doi:10.1046/j.1523-1739.2002.01328.x.
- Begon, M., Harper, J.L., and Townsend, C.R. (1990). *Ecology: individuals, populations and communities*, 2nd ed., Blackwell Scientific Publications, Boston, pp. 945.
- Beissinger, S.R., Walters, J.R., Catanzaro, D.G., Smith, K.G., Dunning, J.H., Haig, S.M., Noon, B.R., and Stith, B.M. (2006). Modeling approaches in avian conservation and the role of field biologists, *Ornithol. Monograph*, 56.
- Betts, M.G., Diamond, A.W., Forbes, G.J., Villard, M.A., and Gunn, J.S. (2006). The importance of spatial autocorrelation, extent and resolution in predicting forest bird occurrence, *Ecol. Model.*, 191, 197-224, doi:10.1016/j.ecolmodel.2005.04.027.
- Bivand, R.S. (2006). Implementing spatial data analysis software tools in R, *Geogr. Anal.*, 38, 23-40, doi:10.1111/j.0016-7363.2005.00672.x.
- Bonham, C.D., and Reich, R. (1999). Influence of spatial autocorrelation on a fixed-effect model used to evaluate treatment of oil spills, *Applied Mathematics and Computation*, 106, 149-162, doi:10.1016/S0096-3003(98)10109-1.
- Burnham, K.P., and Anderson, D.R. (2002). *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*, Springer, New York, pp. 488.
- Burrough, P.A., and McDonnell, R.A. (1998). *Principles of geographical information systems*, Oxford University Press, Inc., New York, pp. 333.
- Bystrak, D. (1981). The North American Breeding Bird Survey, *Studies in Avian Biology*, 6, 34-41.
- Cadman, M.D., Eagles, P.F.J., and Helleiner, F.M. (1987). *Atlas of the breeding birds of Ontario*, University of Waterloo Press, Waterloo, pp. 617.
- Collett, D. (2003). *Modelling binary data*, Chapman & Hall/CRC, New York, pp. 387.
- Conway, C.J. (1999). *The Birds of North America*, No. 421, Canada Warbler (*Wilsonia canadensis*), In: A. Poole and F. Gill (Editors), *The Birds of North America*, Inc., Philadelphia, PA.
- Currie, D.J. (1991). Energy and large-scale patterns of animal and plant-species richness, *Am. Nat.*, 137, 27-49.
- Dechant, J.A., Sondreal, M.L., Johnson, D.H., Igl, L.D., Goldade, C.M., Parkin, B.D., and Euliss, B.R. (1998). *Effects of management practices on grassland birds: Sedge Wren*, Northern Prairie Wildlife Research Center, Jamestown, ND, pp. 17.
- Dobbyn, J., and Couturier, A. (1998). *A comparison of BBS stop locations in Ontario derived from GIS and GPS*, Report prepared by Bird Studies Canada for the Canadian Wildlife Service.
- Elith, J., Burgman, M.A., and Regan, H.M. (2002). Mapping epistemic uncertainties and vague concepts in predictions of species distribution, *Ecol. Model.*, 157, 313-329, doi:10.1016/S0304-3800(02)00202-8.
- Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huetmann, F., Leathwick, J.R., Lehmann, A., Li, J., Lohmann, L.G., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. Overton, J., Peterson, A.T., and Phillips, S.J. (2006). Novel methods improve prediction of species' distributions from occurrence data, *Ecography*, 29, 129-151, doi:10.1111/j.2006.0906-7590.04596.x.
- Environmental Systems Research Institute. (2002). *ArcGIS version 8.3*, Environmental Systems Research Institute, Redlands, California.
- Fielding, A.H., and Haworth, P.F. (1995). Testing the generality of bird-habitat models, *Conserv. Biol.*, 9, 1466-1481, doi:10.1046/j.1523-1739.1995.09061466.x.
- Fielding, A.H., and Bell, J.F. (1997). A review of methods for the assessment of prediction errors in conservation presence/absence models, *Environ. Conserv.*, 24, 38-49.
- Fletcher Jr., R.J. and Koford, R.R. (2002). Habitat and landscape associations of breeding birds in native and restored grasslands, *J. Wildl. Manage.*, 66, 1011-1022.
- Foody, G.M. (2004). Spatial nonstationarity and scale dependency in the relationship between species richness and environmental determinants for the sub-Saharan endemic avifauna, *Global Ecol. Biogeogr.*, 13, 315-320.
- Fortin, M.J. and Dale, M.R.T. (2005). *Spatial analysis: a guide for ecologists*, Cambridge University Press, New York, pp. 365.
- Fotheringham, A.S., Brunson, C., and Charlton, M. (2002). *Geographically weighted regression*, Wiley & Sons, Ltd., Chichester, England, pp. 269.
- Freemark, K., and Collins, B. (1992). *Landscape ecology of birds breeding in temperate forest fragments*, In: J.M. Hagan III and D.W. Johnston (Editors), *Ecology and conservation of Neotropical migrant landbirds*, Smithsonian Institution Press, Washington, pp. 443-454.
- Friedl, M.A., McIver, D.K., Hodges, J.C.F., Zhang, X.Y., Muchoney,

- D., Strahler, A.H., Woodcock, C.E., Gopal, S., Schneider A., Cooper, A., Baccini, A., Gao, F., and Schaaf, C. (2002). Global land cover mapping from MODIS: algorithms and early results, *Remote Sens. Environ.*, 83, 287-302, doi:10.1016/S0034-4257(02)00078-0.
- Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*, Oxford University Press, New York, pp. 266.
- Girard, C., Darveau, M., Savard, J-P.L., and Huot, J. (2004). Are temperate mixedwood forests perceived by birds as a distinct forest type? *Canadian Journal of Forest Research*, 34, 1895-1907.
- Godfrey, W.E. (1966). *The Birds of Canada*, National Museums of Canada, Bulletin No. 203, Ottawa, Canada, pp. 428.
- Guisan, A., and Zimmermann, N.E. (2000). Predictive habitat distribution models in ecology, *Ecol. Model.*, 135, 147-186, doi:10.1016/S0304-3800(00)00354-9.
- Guisan, A., Edwards, T.C., and Hastie, T. (2002). Generalized linear and generalized additive models in studies of species distributions: setting the scene, *Ecol. Model.*, 157, 89-100, doi:10.1016/S0304-3800(02)00204-1.
- H-Acevedo, D., and Currie, D.J. (2003). Does climate determine broad-scale patterns of species richness? A test of the causal link by natural experiment, *Global Ecol. Biogeogr.*, 12, 461-473, doi:10.1046/j.1466-822X.2003.00058.x.
- Halekoh, U., Højsgaard, S., and Yan, J. (2006). The R package gee-pack for generalized estimating equations, *Journal of Statistical Software*, 15, 1-11.
- Harrell Jr., F.E. (2001). *Regression modeling strategies: with applications to linear models, logistic regression, and survival analysis*, Springer, New York, pp. 568.
- Harrell Jr., F.E., Lee, K.L., and Mark, D.B. (1996). Multivariable prognostic models: issues in developing models, evaluating assumptions and adequacy, and measuring and reducing errors, *Stat. Med.*, 15, 361-387, doi: 10.1002/(SICI)1097-0258 (19960229)15:4<361::AID-SIM168>3.0.CO;2-4.
- Hastie, T.J., and Tibshirani, R.J. (1990). *Generalized Additive Models*, Chapman & Hall/CRC, New York, pp. 335.
- Hastie, T.J. (1993). *Generalized additive models*, In: J.M. Chambers and T.J. Hastie (Editors), *Statistical Models in S*, Chapman & Hall, New York, pp. 249-307.
- Herkert, J.R., Kroodsma, D.E., and Gibbs, J.P. (2001). *The Birds of North America*, No. 582, Sedge Wren (*Cistothorus platensis*), in: A. Poole and F. Gill (Editors), *The Birds of North America, Inc.*, Philadelphia, PA.
- Hosmer, D.W., and Lemeshow, S. (2000). *Applied Logistic Regression*, 2nd ed. John Wiley & Sons, Inc. New York, pp. 375.
- Huete, A., Didan, K., Miura, T., Rodriguez, E.P., Gao, X., and Ferreira, L.G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices, *Remote Sens. Environ.*, 83, 195-213, doi:10.1016/S0034-4257(02)00096-2.
- Ihaka, R. and Gentleman, R. (1996). R: a language for data analysis and graphics, *Journal of Computational and Graphical Statistics*, 5, 299-314.
- Irwin, L.L. (1998). *Abiotic influences on bird-habitat relationships*, In: J.M. Marzluff and R. Sallabanks (Editors), *Avian Conservation: Research and Management*, pp.209-217.
- Jetz, W., Rahbek, C. and Lichstein, J.W. (2005). Local and global approaches to spatial data analysis in ecology, *Global Ecol. Biogeogr.*, 14, 97-98, doi:10.1111/j.1466-822X.2004.00129.x.
- Kadmon, R., Farber, O., and Danin, A. (2003). A systematic analysis of factors affecting the performance of climatic envelope models, *Ecol. Appl.*, 13, 853-867.
- Kleinbaum, D.G., and Klein, M. (2002). *Logistic regression: a self-learning text*, 2nd ed. Springer-Verlag New York, Inc. New York, pp. 513.
- Legendre, P. (1993). Spatial autocorrelation: trouble or new paradigm? *Ecology*, 74, 1659-1673.
- Lichstein, J.W., Simons, T.R., Shiner, S.A., and Franzreb, K.E. (2002). Spatial autocorrelation and autoregressive models in ecology, *Ecology*, 72, 445-463.
- Machtans, C.S., and LaTour, P.B. (2003). Boreal forest songbird communities of the Liard Valley, Northwest Territories, Canada, *The Condor*, 103, 27-44.
- McCullagh, P., and Nelder, J.A. (1999). *Generalized linear models*, CRC Press, New York, pp. 511.
- Mitchell, T.D., and Jones, P.D. (2005). An improved method of constructing a database of monthly climate observations and associated high-resolution grids, *Int. J. Climatol.*, 25, 693-712, doi:10.1002/joc.1181.
- Morse, D.H. (2004). Blackburnian Warbler (*Dendroica fusca*). In: A. Poole (Editor), *The Birds of North America Online*. Ithaca: Cornell Laboratory of Ornithology; Retrieved from The Birds of North American Online database: http://bna.birds.cornell.edu/BNA/account/Blackburnian_Warbler/.
- Ontario Partners in Flight. (2006). Ontario Landbird Conservation Plan: Boreal Hardwood Transition (North American Bird Conservation Region 12): priorities, objectives and recommended actions, Version 1.0. EC/MNR.
- Osborne, P.E., and Suarez-Seoane, S. (2002). Should data be partitioned spatially before building large-scale distribution models? *Ecol. Model.*, 157, 249-259, doi:10.1016/S0304-3800(02)00198-9.
- Pearce, J., and Ferrier, S. (2000). Evaluating the predictive performance of habitat models developed using logistic regression, *Ecol. Model.*, 133, 225-245, doi:10.1016/S0304-3800(00)00322-7.
- Peterson, A.T., and Kluza, P.A. (2003). New distributional modelling approach for gap analysis, *Anim. Conserv.*, 6, 47-51, doi:10.1017/S136794300300307X.
- Rich, T.D., C.J. Beardmore, Berlanga, H., Blancher, P.J., Bradstreet, M.S.W., Butcher, G.S., Demarest, D.W., Dunn, E.H., Hunter, W.C., Inigo-Elias, E.E., Kennedy, J.A., Martell, A.M., Panjabi, A.O., Pashley, D.N., Rosenberg, K.V., Rustay, C.M., Wendt, J.S. and Will, C.T. (2004). *Partners in Flight North American Landbird Conservation Plan*, Cornell Lab of Ornithology, Ithaca, NY.
- Robbins, C.S., Bystrak, D., and Geissler, P.H. (1986). *The breeding bird survey: its first fifteen years, 1965-1979*, U.S. Fish & Wildlife Service Publication, No. 157.
- Root, T. (1988). Energy constraints on avian distributions and abundances, *Ecology*, 69, 330-339.
- Segurado, P. and Araujo, M.B. (2004). An evaluation of methods for modelling species distributions, *J. Biogeogr.*, 31, 1555-1568, doi:10.1111/j.1365-2699.2004.01076.x.
- Tucker, C.J., Townshend, J.R.G., and Goff, T.E. (1985). African land-cover classification using satellite data, *Science*, 227, 369-375, doi:10.1126/science.227.4685.369.
- U.S. Geological Survey Survey (1996). GTopo30. <http://edcdaac.usgs.gov/gtopo30/w10090.asp> (accessed June 2005).
- Venier, L.A., McKenney, D.W., Wang, Y., and Kee, J. (1999). Models of large-scale breeding-bird distribution as a function of macroclimate in Ontario, Canada, *J. Biogeogr.*, 26, 315-328, doi:10.1046/j.1365-2699.1999.00273.x.
- Verbeek, N. A. M. and Caffrey, C. (2002). *The Birds of North America*, American Crow (*Corvus brachyrhynchos*). In: A. Poole and F. Gill (Editors), *The Birds of North America, Inc.*, Philadelphia, PA, No. 647.
- Wang, Q., Ni, J., and Tenhunen, J. (2005). Application of a geographically-weighted regression analysis to estimate net primary production of Chinese forest ecosystems, *Global Ecol. Biogeogr.*, 14, 379-393, doi:10.1111/j.1466-822X.2005.00153.x.

- Williams, E.J., and Pashley, D.N. (1999). Designation of conservation planning units. In: R. Bonney, D.N. Pashley and L. Niles (Editors), *Strategies for bird conservation: the Partners in Flight planning process*. <http://birds.cornell.edu/pifcapemay>, Cornell Lab of Ornithology.
- Wootton, J.T. (1996). *The Birds of North America*, Purple Finch (*Carpodacus purpureus*). In: A. Poole and F. Gill (Editors), *The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, D.C.*, No. 208.
- Wu, H., and Huffer, F.W. (1997). Modelling the distribution of plant species using the autologistic regression model, *Environ. Ecol. Stat.*, 4, 49-64.
- Yan, J. (2002). geepack: yet another package for generalized estimating equations, *R News*, 2-3, 12-14.
- Young, L., Betts, M.G., and Diamond, A.W. (2005). Do Blackburnian Warblers select mixed forest? The importance of spatial resolution in defining habitat, *For. Ecol. Manage.*, 214, 358-372, doi:10.1016/j.foreco.2005.04.022.
- Zhang, L., Gove, J.H., and Heath, J.S. (2005). Spatial residual analysis of six modeling techniques, *Ecol. Model.*, 186, 154-177, doi:10.1016/j.ecolmodel.2005.01.007.
- Zweig, M.H., and Campbell, G. (1993). Receiver-operating characteristic (ROC) plots: a fundamental evaluation tool in clinical medicine, *Clin. Chem.*, 39, 561-571.